

FLORA OF PANAMA¹

Part VIII

FAMILY 149. ERICACEAE³

BY ROBERT L. WILBUR² AND JAMES L. LUTEYN³

Trees, shrubs, woody vines or herbs (the latter occasionally fleshy myco-parasites although often allegedly saprophytic). *Leaves* alternate but rarely opposite or whorled, simple, estipulate, coriaceous and persistent to membranous and deciduous; leaf scars usually with a single vascular bundle scar, nodes usually with one trace and one gap. Inflorescences basically racemose (either racemes, panicles, corymbs or flowers solitary); pedicels bibracteolate, subtended by a deciduous or persistent bract. *Flowers* mostly bisexual but rarely functionally unisexual (more rarely plants dioecious), actinomorphic or slightly zygomorphic; mostly (4-)5(-7)-parted, typically obdiplostemonous, hypogynous or epigynous and with a typically biseriate perianth; sepals occasionally distinct or more typically calyx 4-5(-7)-lobed, often persistent, valvate, imbricate or reduplicate in bud; corolla occasionally distinct but more typically of 4-5(-7) united petals, commonly funnelform, campanulate or urceolate, and valvate, convolute or imbricate in bud; stamens usually twice as many as the petals (or rarely just as many), borne on the edge of a nectariferous disc or rarely epipetalous, distinct or united, the anthers 2-celled, apparently inverting during development, dehiscing longitudinally or more typically by apical clefts or pores, often with distinct or connate tubules and often with terminal awns or abaxial spurs, pollen grains in tetrads or less frequently single (Monotropoideae); pistil (2)4-5(10)-carpellate; stigma simple but occasionally weakly lobed, the style single, the ovary 1, superior or inferior, usually with as many locules as carpels or with twice as many locules as carpels or rarely loculate in lower portion and 1-locular above the placentation axile, the ovules numerous or rarely solitary, anatropous to campylotropous with a single integumentary layer. *Fruit* a loculicidal or septicidal capsule, berry or drupe with a usually persistent, rarely accrescent and fleshy calyx; seeds usually small, anatropous, rarely winged or tailed.

The Ericaceae is a family of about 100 genera and perhaps 3,000 species,

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² Department of Botany, Duke University, Durham, North Carolina 27706.

³ The New York Botanical Garden, Bronx, New York 10458.

widely distributed in the temperate regions of both hemispheres and in the tropics where it is more abundant in the mountains.

Literature:

- Drude, O. 1889. Ericaceae. In A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien IV, 1: 15–65.
- Sleumer, H. 1941. Vaccinioideen-Studien. Bot. Jahrb. Syst. 71: 375–510.
- Small, J. K. 1914. Ericaceae. N. Amer. Fl. 29: 33–102.
- Smith, A. C. 1932. The American species of Thibaudieae. Contr. U.S. Natl. Herb. 28: 311–547.
- Standley, P. C. & L. O. Williams. 1966. Ericales in Flora of Guatemala. Fieldiana, Bot. 24(pt. 8): 73–127.
- Stevens, P. F. 1971. A classification of the Ericaceae: subfamilies and tribes. J. Linn. Soc. Bot. 64:1–53.
- Wood, Carroll E., Jr. 1961. The genera of the Ericaceae in the Southeastern United States. J. Arnold Arbor. 42: 10–80.

KEY TO THE GENERA

- a. Leaves whitish, pinkish or reddish or at least not green (i.e. lacking chlorophyll); plants herbaceous, succulent 12. *Monotropa*
- aa. Leaves green; plants woody shrubs or trees.
 - b. Petals distinct; fruit a 6–7 locular, septicidally dehiscent capsule 4. *Befaria*
 - bb. Petals united; fruit a berry, drupe or if a capsule, then loculicidal.
 - c. Ovary superior.
 - d. Anther sacs (thecae) each terminated by 2, ascendent to erect awns; calyx lobes either closely appressed to base of fruit or becoming somewhat succulent and accrescent at maturity; fruit a berry or capsule, many seeded, with a smooth or pubescent surface but never beset with columnar projections.
 - e. Calyx neither becoming succulent in fruit nor enveloping the berry, calyx lobes in fruit less than $\frac{1}{4}$ length of the berry; flowers solitary in the axils of the upper leaves 13. *Pernettya*
 - ee. Calyx becoming somewhat succulent in fruit accrescent, and closely enveloping the basal $\frac{2}{3}$ of the capsule; calyx lobes in fruit more than $\frac{1}{2}$ the length of the capsule; flowers in terminal or axillary racemes or panicles 8. *Gaultheria*
 - dd. Anther sacs (thecae) each bearing a single reflexed or dorsally spreading awn; calyx lobes never becoming fleshy and either spreading or reflexed; fruit a drupe with 4–10, seed-like nutlets and with the surface always densely beset with columnar projections 3. *Arctostaphylos*
 - cc. Ovary inferior.
 - f. Hypanthium continuous with the pedicel, the pedicel not jointed.
 - g. Hypanthium winged or angled.
 - h. Flowers solitary; corolla 1 cm long or less; pedicels shorter than the flowers, less than 3 mm long, bibracteolate; stamens less than 5 mm long; corolla unwinged 17. *Themistoclesia*
 - hh. Flowers in 2–4-flowered racemes; corolla 1.5 cm long or more; pedicels as long as the flowers, ca. 15 mm long or longer, ebracteolate; stamens ca. 10 mm long; corolla 5-winged 2. *Anthopterus*
 - gg. Hypanthium wingless.
 - i. Flowers and fruits borne on slender, elongate pedicels equaling or longer than the subtending leaves.
 - j. Calyx 10 mm or longer; corolla 20 mm long or longer; stamens 10 mm long or longer 6. *Didonica*

- jj. Calyx 4 mm long or less; corolla 6(-12) mm long or less; stamens 5(-9) mm long or less — 16. *Sphyrospermum*
- ii. Flowers and fruits borne on pedicels much shorter than the subtending leaves — 19. *Vaccinium*
- ff. Hypanthium disarticulating from the pedicel, the pedicel clearly jointed just below the flower.
 - k. Calyx basally clasped by 2, ovate, pedicellary bractlets so as to be largely hidden from view; pedicels less than 2 mm long — 7. *Disterigma*
 - kk. Calyx not basally clasped by 2, ovate, pedicellary bractlets and not largely hidden by them; pedicels mostly more than 2 mm long.
 - l. Anthers dehiscing by longitudinal slits extending for much of the length of the anther sacs; tubules rudimentary, less than 0.4 mm long — 9. *Lateropora*
 - ll. Anthers dehiscing by pores or clefts on the tubules, these not extending onto the anther sacs; tubules well developed, 1 mm long or longer.
 - m. Stamens with filaments and anthers all of the same length.
 - n. Anther sacs rigid and coarsely granular; tubules rigid.
 - o. Anther connectives unspurred; tubules united completely with a single passage or laterally connate but with 2 passages or rarely distinct to their bases — 11. *Macleania*
 - oo. Anther connectives all or alternately laterally spurred; tubules distinct to their bases — 14. *Psammisia*
 - nn. Anther sacs flexible and smooth or finely granular; tubules flexible.
 - p. Anthers spurless.
 - q. Inflorescence paniculate; filaments connate; corolla white or pinkish — 18. *Thibaudia*
 - qq. Inflorescence corymbose; filaments distinct; corolla greenish or greenish yellow — 19. *Vaccinium*
 - pp. Anthers dorsally spurred.
 - r. Leaves 5-plinerved, entire; hypanthium conspicuously 5-winged — 1. *Anthopteropsis*
 - rr. Leaves pinnately veined, serrulate; hypanthium wingless — 19. *Vaccinium*
 - mm. Stamens, filaments or anthers or both alternately unequal, obviously of 2 lengths.
 - s. Filaments clearly unequal in length, distinct or rarely weakly coherent at the very base.
 - t. Calyx lobes 5, less than 1 cm long; anthers alternately unequal in length; stamens more than half as long as the corolla, floral bracts usually longer than 10 mm and always at least 3 mm long — 5. *Cavendishia*
 - tt. Calyx lobes 3, 1.5 cm long or longer; anthers equal in length; stamens about $\frac{1}{3}$ as long as the corolla; floral bracts ca. 1.5 mm long — 10. *Lysiclesia*
 - ss. Filaments of equal length, connate for their entire length — 15. *Satyria*

1. ANTHOPTEROPSIS

Anthopteropsis A.C. Smith, Ann. Missouri Bot. Gard. 28: 441. 1941. TYPE: *A. insignis* A.C. Smith.

Epiphytic *shrubs*. *Leaves* short petiolate, subcoriaceous, plinerved, entire. *Inflorescences* terminal or rarely axillary, racemose, with the 5–12 flowers borne on medially bibracteolate pedicels subtended by a minute papery bract and articulated with the hypanthium. *Flowers* with the hypanthium fleshy, subglobose, conspicuously and broadly 5-winged to the sinuses, calyx limb erect, the lobes 5, inconspicuous, toothlike and minutely apiculate; corolla tube fleshy, cylindric, inconspicuously 5-angled, the lobes small, deltoid; stamens 10, equal, about half as long as the corolla, the filaments distinct, membranaceous, the anthers inserted dorsally near the base, the thecae slightly to coarsely granular, basally short appendaged, the connectives alternately medially and dorsally spurred, the tubules flexible, dehiscent over their entire length by elongate clefts; style filiform, equalling or slightly exceeding the corolla tube, the ovary inferior, 5-loculate, crowned with an annular disc. *Fruit* a berry.

Anthopteropsis is a monotypic genus endemic to central Panama. It is allied to *Macleania* and especially to *Psammisia*. Its alternately and inconspicuously spurred anthers are similar to those of some South American species of *Psammisia*. Additional collections and further study might suggest its inclusion in *Psammisia*.

1. ***Anthopteropsis insignis*** A.C. Smith, Ann. Missouri Bot. Gard. 28: 441. 1941.
TYPE: Panama; Coclé, El Valle de Antón, Allen 2500 (A, holotype; MO, isotype).—FIG. 1.

Epiphytic *shrub* to 4 m tall, mature branches terete, glabrous; bark grayish when dry, cracking longitudinally; immature branches and twigs of new growth subterete or bluntly angled, somewhat striate, puberulous, yellowish or reddish brown when dry. *Leaves* coriaceous, elliptic to oblong elliptic, (3–)4.5–6 cm long, (1.5–)2–3 cm wide, basally rounded, narrowly rounded or subcordate, apically subacute, rounded, obtuse or bluntly short acuminate, glabrous except puberulous along the nerves above; 3(–5)-plinerved, the midrib, the lateral nerves and the veinlets reticulate, all raised slightly on both the surfaces; petioles subterete, slightly flattened above, puberulous, 2–3 mm long and 2 mm in diameter. *Inflorescence* 5–8(–12)-flowered; rachis coarsely angled, striate, glabrous, 2–13 mm long; floral bracts ovate to deltoid, acuminate to subacute, ca. 1.5 mm long, ca. 2 mm wide, marginally glandular fimbriate; pedicels subterete, rugulose, swollen distally, 10–20 mm long, 1–2 mm in diameter, inconspicuously puberulous and with scattered glandular fimbriae distally; bracteoles ovate to deltoid, acuminate to subacute, ca. 1–1.5 mm long, 1 mm wide, marginally glandular fimbriate, located at the middle of the pedicel. *Flowers* with the hypanthium fleshy, glabrous, bright pink to red, (5.5–)6–9 mm long, 8–10 mm in diameter including wings, the tube 4–5 mm long, the limb 3–4 mm long, the lobes apiculate, the wings 1.5–2(–3) mm broad and conspicuously veined, corolla cylindric, angled but not winged, yellow, glabrous but often with scattered glandular fimbriae, (16.5–)17–19 mm long, 3–4 mm in diameter, the lobes 1.0–2.0 mm long, 2.0–2.5 mm wide, flaring at anthesis; stamens 9–10.5 mm long, the filaments distinct but often adnate to base of the corolla tube, 2.0–3.0 mm long, 1.3 mm wide

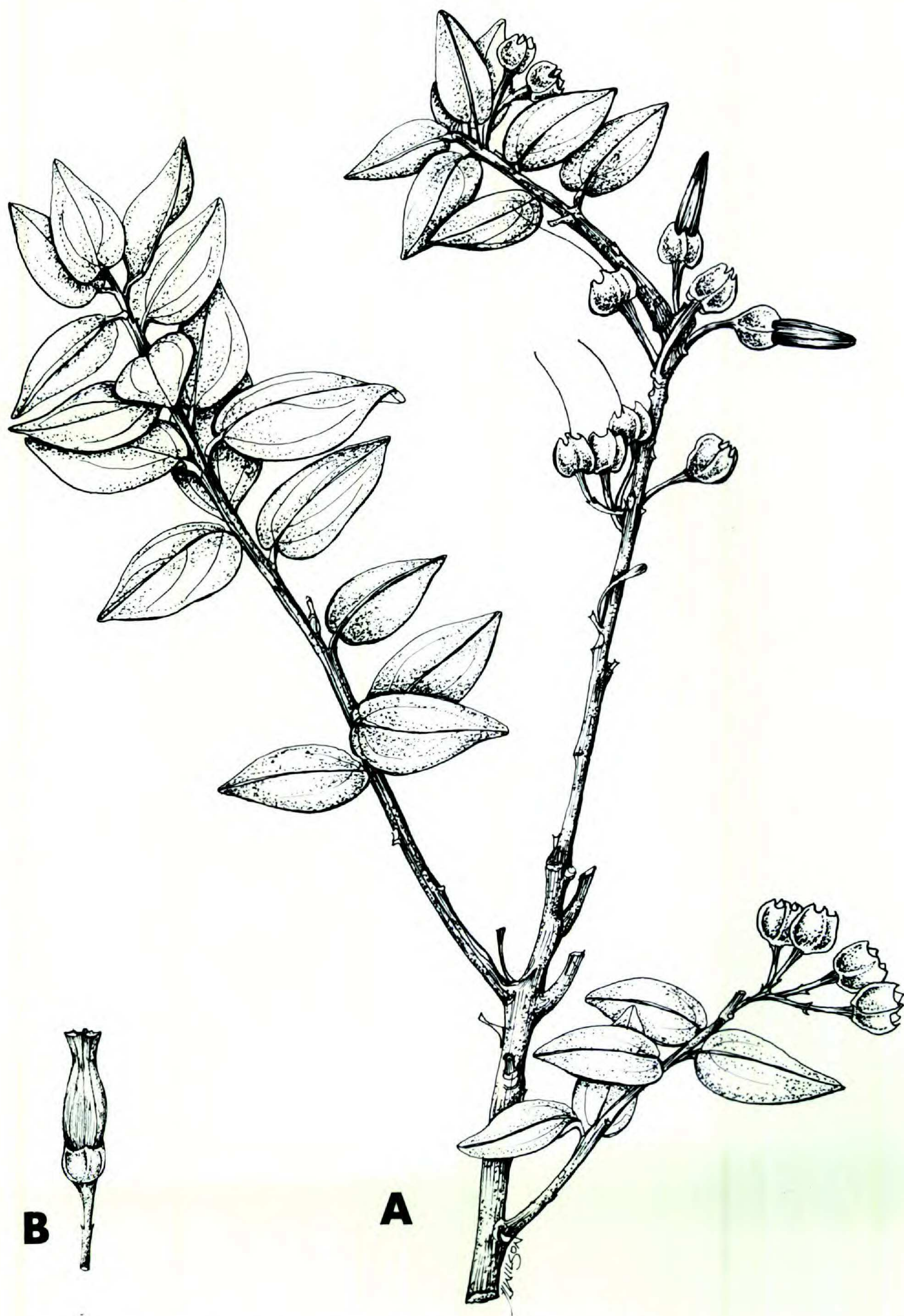


FIGURE 1. *Anthopteropsis insignis* A. C. Smith.—A. Habit ($\times 7/10$).—B. Flower ($\times 7/8$).
[After Allen 2946 (MO).]

at the base, marginally pilose distally and onto the connective, the anthers 7–9 mm long, the thecae 4.0–5.5 mm long, with a short, caudate, occasionally pubescent, basal appendage, the tubules flexible, acute, slightly narrower than the thecae, dehiscent over the entire length; style exserted, 18–20 mm long. *Berry* red, 7–9 mm long.

COCLÉ: Hills S of El Valle de Antón, 700 m, *Allen* 2500 (A, MO). Region S of El Valle de Antón, 700 m, *Allen* 2946 (A, F, GH, MO, NY, US). Hills N of El Valle de Antón, *Allen* 3556 (F, GH, MO, NY, US). PANAMÁ: Cerro Jefe 700 m, *Dressler* 3680 (DUKE, PMA). Road past Cerro Azul, 20 km from Interamerican Highway, *Mori & Kallunki* 2212 (MO). El Llano-Cartí Road, 9 km from Interamerican Highway, 350 m, *Mori & Kallunki* 5157 (MO).

2. ANTHOPTERUS

Anthopterus Hook., Icon. Pl. 3: *pl.* 243. 1840. TYPE: *A. racemosus* Hook.

Low *shrubs* or small *trees*. *Leaves* alternate but occasionally appearing subopposite, petiolate, coriaceous, plinerved or pinnatinerved, entire. *Inflorescence* axillary, racemose, with several to many flowers; floral bracts solitary at base of pedicel, to 20 mm long but usually small and inconspicuous; pedicels either naked or more typically bibracteolate, continuous with the flower. *Flowers* with the hypanthium prismatic, broadening distally and winged opposite the sinuses; calyx limb suberect, the lobes 5, lanceolate triangular; corolla subcylindric, cylindric urceolate or subglobose, broadly 5-winged opposite the lobes, the lobes triangular, subacute; stamens 10, equal, nearly as long as the corolla, the filaments equal, membranous, distinct or basally slightly connate or connate for half their length, the anthers dorsifixed, membranous with smooth thecae, the tubules usually longer than the anther sacs and opening by short to elongate, introrse clefts; ovary inferior, the stigma truncate, the style filiform, about as long as the corolla, basally surrounded by an annular or cupuliform disc. *Fruit* a berry with numerous small seeds.

Anthopterus is a genus of about five species ranging from eastern Panama to northeastern Peru. There are few collections of any of the species and hence the range of variation within the genus is unknown. *Anthopterus* is closely related to *Thibaudia* and is traditionally separated from that genus by the conspicuously winged calyx and corolla of the former genus in contrast to the wingless or merely angulate calyx and corolla of *Thibaudia*.

1. **Anthopterus wardii** Ball, Hook. Icon. Pl. 15: *pl.* 1465. 1884. TYPE: Colombia: Dept. of El Valle: Buenaventura, near sea level, *Ward s.n.* (K, holotype, not seen).—FIG. 2.

Thibaudia wardii (Ball) Hoerold, Bot. Jahrb. Syst. 42: 274. 1909.

Epiphytic *shrub* or low *tree*; mature branches terete, glabrate; immature branches and twigs of new growth terete, puberulous, tan when dry. *Leaves* oblong or ovate oblong to lance elliptic, 6–13 cm long, 2.5–6 cm wide, basally subcordate, bluntly acuminate, puberulous proximally along the midrib above, glabrous elsewhere, entire, the margin slightly revolute, 5–7-plinerved, the secondary veins originating near the base and the midvein flush or slightly impressed

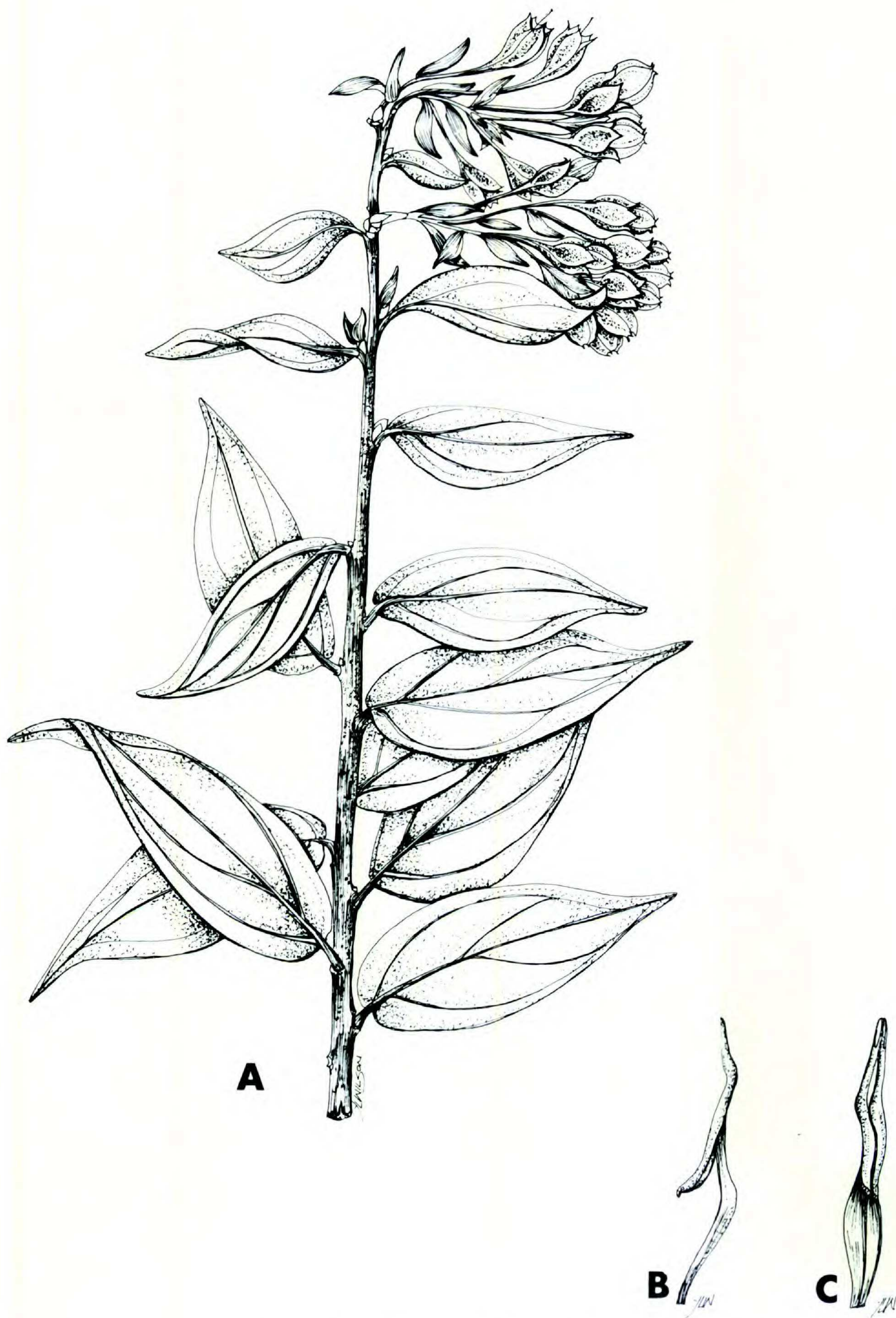


FIGURE 2. *Anthopterus wardii* Ball.—A. Habit ($\times \frac{3}{5}$).—B-C. Stamens.—B. Lateral view ($\times 5$).—C. Ventral view ($\times 5$). [After Archer 1901 (NY), Colombia.]

above, prominently elevated beneath, the veinlets copiously reticulate and slightly raised on both the surfaces; petioles subterete, flattened above, puberulent, 3–5 mm long, 1.5–2 mm in diameter. *Inflorescence* axillary, short racemose with usually ca. 4 flowers; rachis subterete basally, 1–2 cm long, basally surrounded by several triangular to oblong bracts 3–5 mm long; pedicels subterete basally but becoming winged distally, striate, glabrous, 10–20 mm long, each subtended by an oblong bract 3–6 mm long with scattered glandular fimbriae; bracteoles lacking. *Flowers* glabrous; hypanthium urceolate to obprismatic, ca. 8–9 mm long, the wings ca. 1–1.5 mm wide, the limb subspreading, 8–9 mm long including the lobes; calyx lobes triangular ovate, acute, 5–7 mm long, 4–5 mm wide at the base, ca. 7 parallel, branching veins not quite extending to the margin; corolla white, membranous when dry, 10–14 mm long, ca. 16 mm in diameter at the widest point, slightly contracted at both the base and apex and with semiobovate wings 2–5 mm wide, a single longitudinal vein parallel to the margin, the lobes ovate, apiculate, ca. 1 mm wide; stamens 8–10 mm long, the filaments ca. 4 mm long, membranous, connate for about $\frac{1}{2}$ their length, adnate to the corolla; anther sacs ca. 2 mm long, gradually tapering into flexible tubules ca. 3 mm long and opening by introrse clefts about $\frac{1}{2}$ the length of the tubule; stigma truncate.

Anthopterus wardii ranges along the Pacific slope of the Western Cordillera of the Andes from eastern Panama (Darién) into Ecuador. It occurs from near sea level to 1,200 m altitude.

DARIÉN: Cerro Pirre, *Bristan* 610 (MO); *Bristan* 611 (MO). Cloud forest or mossy forest, Cuasí-Caná; trail between Cerro Campaniento and La Escalera to "Paramo" E of Tres Bocas, *Kirkbride* 1308 (MO). Crest of the Cañá-Cuasí Trail, 5500 ft, *Terry* 1569 (F).

3. ARCTOSTAPHYLOS

Arctostaphylos Adans., *Fam. Pl.* 2: 165. 1763. nom. conserv. TYPE: *A. uva-ursi* (L.) K.P.J. Sprengel.

Uva-Ursi [Tourn.] Miller, *Gard. Dict. abr. ed.* 4. 1754.

Comarostaphylis Zucc., *Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss.* 2: 331. 1837. TYPE: *C. arguta* Zucc.

Xerobotrys Nutt., *Trans. Am. Philos. Soc. ser. 2.* 8: 267. 1843.

Xylococcus Nutt., *Trans. Am. Philos. Soc. ser. 2.* 8: 258. 1843. TYPE: *X. bicolor* Nutt.

Daphnidostaphylis Klotzsch, *Linnaea* 24: 79, 87. 1851.

Arctous (A. Gray) Niedenzu, *Bot. Jahrb. Syst.* 11: 180. 1889. TYPE: *A. alpina* (L.) Niedenzu.

Ornithostaphylos Small, *N. Amer. Fl.* 29: 101. 1914. TYPE: *O. oppositifolia* (Parry) Small.

Schizococcus Eastw., *Leafl. W. Bot.* 1: 98. 1934. TYPE: *S. nummularia* (A. Gray) Eastwood.

Shrubs or small *trees* with diffuse to prostrate or erect stems. Leaves persistent or rarely deciduous, usually coriaceous, rarely membranous, often revolute, entire, undulate or toothed, pinnately veined, petiolate or sessile. *Inflorescence* of few to numerous flowers borne in terminal, solitary or clustered, racemelike panicles; pedicels slender, bibracteolate at or near the base, each subtended by a persistent or deciduous bract. *Flowers* with the calyx persistent with (4)5 nearly distinct lobes much longer than the calyx tube, spreading or reflexed at maturity; corolla urceolate, cylindric, ovoid, globular to somewhat campanulate, (4)5-lobed and the lobes often recurved or spreading; stamens (8)10, included, the filaments dilated and usually basally pubescent, the anthers introrse, each

anther sac with a recurved dorsal hornlike spur, the thecae opening by introrse terminal pores; stigma minute or slightly capitate dilated, the style slender to columnar, ovary superior on a hypogynous disc, (2-)4-5(-10) celled. *Drupe* globose, usually fleshy but rarely dry, the pericarp smooth to papillose or warty; nutlets 4-10, seedlike, each with a solitary seed, the nutlets irregularly separable or united into a solid stone.

Arctostaphylos when broadly interpreted is a genus of about 50 species with one species circumboreal and the remainder mostly restricted to western North and Central America. The genus is broadly circumscribed here to include all those members of the tribe Arbutae with a solitary seed in each locule. The southern Central American representatives all belong to the segregate genus *Comarostaphylis* which is characterized by fleshy drupes with a papillate pericarp surrounding a solid stone of 3-5 locules and a single seed within each compartment. In contrast to the broader generic usage adopted here, *Arctostaphylos* is often restricted to include only those species with a more or less smooth, nonpapillate pericarp.

1. ***Arctostaphylos arbutoides*** (Lindl.) Hemsl., Biol. Centr. Amer., Bot. 2: 278. 1881.—FIG. 3.

Comarostaphylis arbutoides Lindl., Bot. Reg. 29, pl. 30. 1843. TYPE: plants grown in London from seed gathered at Quezaltenango, Guatemala, not seen.

Comarostaphylis chiriquensis Camp, Ann. Missouri Bot. Gard. 26: 297. 1939. TYPE: Panama, Chiriquí, Volcán de Chiriquí, Woodson *et al.* 1033 (NY, holotype; MO, NY, isotypes).

Comarostaphylis sleumeri Suessenguth, Bot. Jahrb. Syst. 72: 282. 1942. [as *Comarostylis*]. TYPE: Costa Rica, Chirripó, 3400-3837 m, Kupper 1319, 1173 (M, syntypes).

Bushy *shrub* or small *tree* 1-4(-5) m tall; young branchlets moderately to densely puberulous, often also sparsely to moderately but inconspicuously glandular pubescent, the pubescence often giving an overall ferrugineous or grayish appearance. *Leaves* coriaceous, elliptic to oblong or oblanceolate, (3-)5-7(-9) cm long, ca. (0.8-)1.0-2.5(-3.0) cm wide, apically acute and tapering basally, while immature moderately flocculent above with ferrugineous, crispy trichomes, glabrous and shiny at maturity, moderately to densely grayish or ferrugineously tomentulose beneath, marginally entire to obscurely undulate, somewhat revolute, the midvein and the primary lateral veins somewhat impressed above and elevated beneath; petioles mostly 4-12 mm long, terete, channeled above, grayish to ferrugineous puberulous but often glabrescent. *Inflorescence* terminal, densely paniculate, the rachis and the inflorescence branches moderately but inconspicuously puberulous, often also with a pilose scattering of gland-tipped, short trichomes; pedicels terete, (1-)1.5-3.0(-5) mm long, densely puberulous, often with gland-tipped, short trichomes subtended by a bract and bracteoles, the bract slightly keeled, deltoid to elliptic, 2.0-3.5 mm long, adaxially glabrous, abaxially puberulous, often sparingly beset with gland-tipped short trichomes, the bracteoles 2, nearly medial, linear to lanceolate, abaxially puberulous, acute, 1.5-2.5 mm long. *Flowers* with the calyx lobes 5, 1.5-2.0 mm long, deltoid to triangularly ovate, acute, adaxially puberulous; corolla urceolate, creamy white or pale yellow, mostly 5-6(-7) mm long, ca. 3.5-4.5 mm in diam., externally

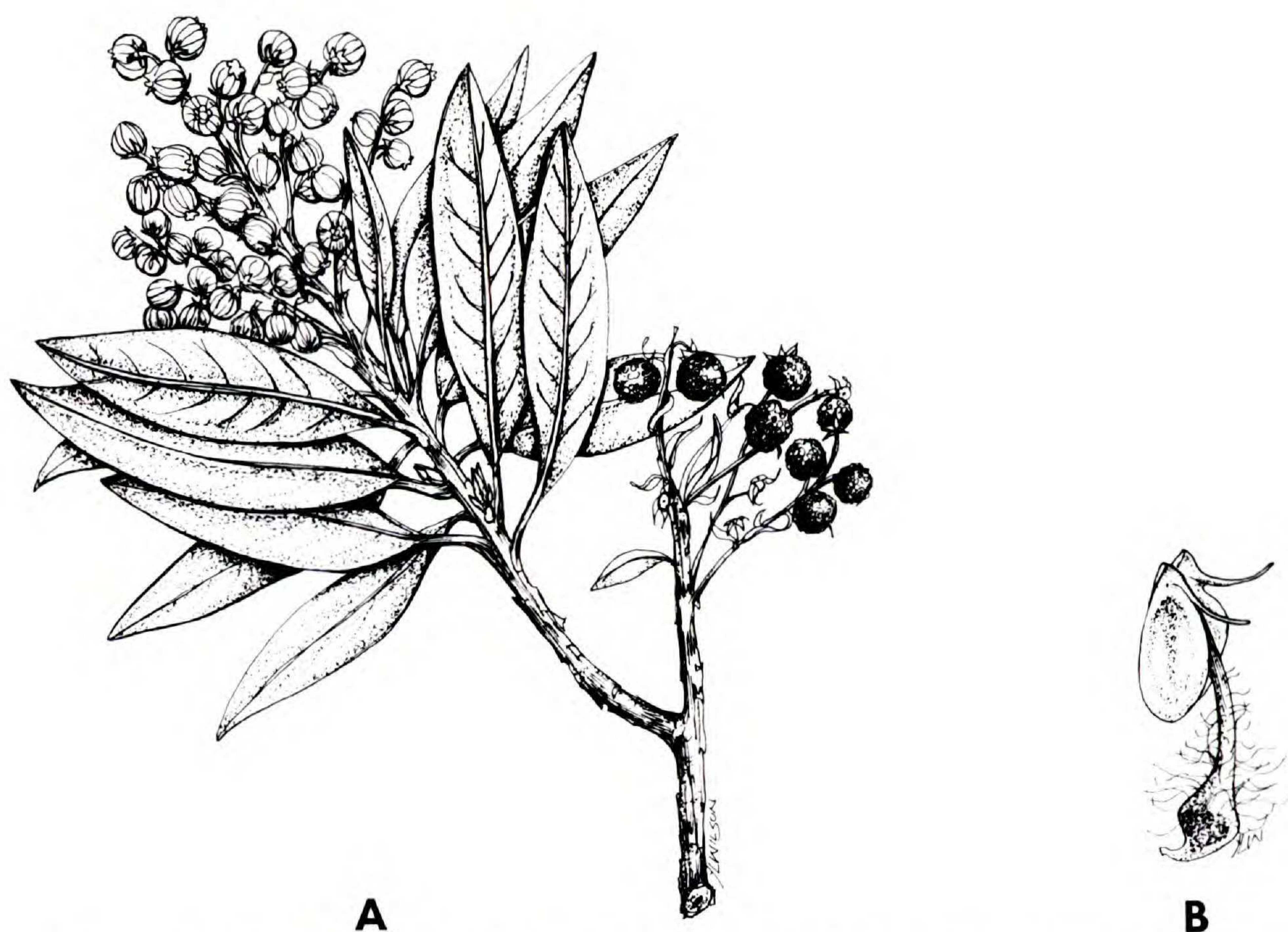


FIGURE 3. *Arctostaphylos arbutoides* (Lindl.) Hemsl.—A. Habit ($\times \frac{3}{5}$).—B. Stamen, lateral view ($\times 10$). [After Wilbur *et al.* 15412A (DUKE).]

glabrous to indistinctly and finely puberulous or pilosulose, the lobes shallowly oblong, apically undulate, 0.5–0.7 mm long, ca. 1.5 mm wide, spreading to recurved; stamens 10, 2.5–3.0 mm long, the filaments arching, basally swollen, pilosulose, the anthers attached medially, 2.0–2.5 mm long, the anther sacs 1.0–1.3 mm long with dorsal spurs ca. 0.5 mm long; stigma slightly broader than the style, style glabrous, 2.5–3.0 mm long, 0.5–0.7 mm in diam., the ovary glabrous or pilosulose, soon glabrate, verruculose. *Drupe* ovoid to globose, glabrous, conspicuously warty, 4–6(–7) mm in diameter.

This is a widespread species, highly variable, especially in the type and distribution of pubescence. The species apparently ranges from southern Mexico southward into Panama. The synonyms listed above are based on minor variations in pubescence and are not worthy of formal taxonomic status. A Costa Rican variant which occurs on Volcán Irazú is recognized as var. *costaricensis*.⁴

The var. *costaricensis* is apparently the only variant occurring on Volcán Irazú. A collection is known from Alajuela Province from Palmira, *Austin Smith* P2239 (A). Its range appears to be restricted to the Cordillera Central. The

⁴ *Arctostaphylos arbutoides* var. *costaricensis* (Small) Wilbur & Luteyn, comb. nov. *Comarostaphylis costaricensis* Small, N. Amer. Fl. 29: 89. 1914. TYPE: Costa Rica, Prov. de Cartago, Volcán Irazú, O. Kuntze 2361 (NY). *Arctostaphylos costaricensis* (Small) Standley, Fieldiana, Bot. 4: 320. 1929. Young branchlets glabrous. Leaves glabrous beneath or nearly so. Rachises glabrous to moderately glandular pubescent. Calyx lobes glabrous or merely ciliate.

more widespread typical variety has puberulent branchlets, leaves moderately to densely ferrugineous beneath and densely puberulent calyx lobes. In southern Central America it is found in the Talamanca Range of Costa Rica and Panama.

CHIRIQUÍ: Summit and SW face of Cerro Copete, 9000 ft, *Allen* 4888 (MO, US). Llano del Volcán, 1500–1600 m, *Allen & Fairchild* 3460 (F, MO, NY, US). Volcán Barú, E slopes along road to summit, 1 mi. from summit, 3000 m, *Croat* 34914 (MO). Summit of El Barú, 3225–3447 m, *Croat* 34929 (MO). Upper rim of Potrero Muleto, *Croat* 34949 (DUKE). Roadside, Potrero Muleto to summit of El Barú, *D'Arcy* 10154 (DUKE, MO). Top of peak between Barú and Respinga, ca. 3000 m, *D'Arcy* 10096 (DUKE, MO, NY). E slope of Volcán de Chiriquí (Barú), WNW of Boquete, 1900–2000 m, *Davidse & D'Arcy* 10166 (DUKE, MO, NY). Elfin forest on ridges above Potrero Muleto, 11 km WNW of Boquete on W slope of Volcán de Chiriquí, *Davidse & D'Arcy* 10259 (MO, NY). Lava flow 3 km NE of El Hato del Volcán, *Davidse & D'Arcy* 10405 (MO, NY). Volcán de Chiriquí, Boquete District, 7000 ft, *Davidson* 906 (A, F, US); 9000 ft, *Davidson* 974 (A, F), 11500 ft, *Davidson* 1292 (F); 3000 m, *Gutierrez* (PMA); 3600 m, *Killip* 3594 (US). Wooded slopes 6.7 mi W of Boquete, 8000 ft, *Luteyn* 1489 (DUKE, MO). Moist summit of Cerro de Lino above El Boquete, 1560 m, *Maxon* 5210a (US). W side of Volcán Barú, 2000–2500 m, *Mori & Bolten* 7365 (MO); 1500 m, *Mori & Kallunki* 5694 (DUKE, MO). Forest of Cerro de Lino, above El Boquete, 1300–1560 m, *Pittier* 3038 (US). Volcán de Chiriquí, *Pittier* 3095 (F, US); *Sapper* s.n. (US); 11000 ft, *Terry* 1292 (A, MO). Potrero Muleto, Volcán de Chiriquí, Boquete, 10400 ft, *Terry* 1312 (A, F). Dry windswept canyon bottom, 8 mi NE of El Volcán, 8100–8400 ft, *Tyson* 836 (FSU, MO). W slope of El Barú, 6000–7000 ft, *Tyson & Loftin* 5956 (FSU); above 11000 ft, *Tyson & Loftin* 6156 (FSU, MO). Top of El Barú, *Tyson & Loftin* 6166 (FSU, MO). Lava flow NE of El Hato del Volcán near Aguacate, *Wilbur et al.* 10964 (DUKE, MO, PMA, US). Old lava field 4 mi NE of El Hato del Volcán near Río Macho del Monte; 1800 m, *Wilbur et al.* 13065 (DUKE, MO); 1950 m, *Wilbur et al.* 15412A (DUKE, PMA, US); 6200 ft, *Wilbur et al.* 17222 (DUKE). Potrero Muleto to summit of Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery* 413 (NY). Loma Larga to summit, Volcán de Chiriquí, 2500–3380 m, *Woodson et al.* 1033 (MO, NY).

4. BEFARIA

Befaria Mutis ex L., Mant. 2: 152, 242. 1771. TYPE: *B. aestuans* L.

Acunna Ruiz & Pavón, Fl. Peruv. Chil. Prodr. 69, pl. 12. 1794.

Jurgensenia Turczaninov, Bull. Soc. Imp Naturalistes Moscou 20: 151. 1847. TYPE: *J. mexicana* Turcz.

Shrubs or small, slender *trees*, glabrous to densely glandular setose. *Leaves* alternate, petiolate, persistent, entire or rarely obscurely denticulate, the margins flat to tightly revolute. *Inflorescence* terminal or axillary, racemose to corymbose, few to many flowered, often viscid. *Flowers* with the calyx campanulate, (5)7 (8)-parted, the lobes persistent; corolla of (5)7(8) distinct, showy petals, these imbricate in bud, the odd petal abaxial, white to pinkish or red, suberect or slightly spreading at anthesis, soon deciduous; stamens twice as many as the petals or more (10–20), about as long as the petals, the filaments free, distinct, elongate, basally dilated and densely pilose, the anthers oblong obconic, dorsifixed, slightly awned, obliquely 2-pored at the apex; stigma capitate, 7-grooved, the style terete, glabrous, elongate and often bent to one side; ovary superior, glabrate, 6–7-locular, the numerous ovules borne on a conspicuous axile placenta. *Capsule* subglobose, septicidally 7-valvate from the apex; many-seeded.

Befaria is a difficult genus of perhaps 25 highly variable species, ranging from Georgia and Florida to Cuba, and from Mexico south into Bolivia. The most re-

cent revision of the genus (Mansfeld & Sleumer, 1935) is unsatisfactory due to the extreme variation encountered in such "key" characters as plant indumentum and corolla size. One species has recently been found in Panama.

Literature:

- Camp, W. H. 1941. Studies in the Ericales. A discussion of the genus *Befaria* in North America. Bull. Torrey Bot. Club 68: 100–111.
Mansfeld, R., and H. Sleumer. 1935. Revision der Gattung *Befaria* Mutis. Notizbl. Bot. Gart. Berlin-Dahlem 12: 235–276.

1. ***Befaria glauca*** Humboldt & Bonpland, Pl. Aeq. 2: 118, *pl.* 117. 1809 [1813].
TYPE: Venezuela, *Bonpland* 644 (Herb. Willd. no. 9124) (P, holotype?; B, isotype, neither seen)—FIG. 4.

Tree 5–6 m tall, mature stems glabrous, terete; bark grayish black, cracking reticulately; immature branches coarsely ribbed, glabrous but becoming densely ferrugineous tomentose at the tips of the new growth. *Leaves* lance elliptic, 2–4.5 cm long, 0.8–1.5 cm wide, basally cuneate and decurrent, apically acute, apiculate, glabrous on both the surfaces when mature, younger leaves weakly ferrugineous tomentose along the midrib on both the surfaces, lamina dark olive green above and pale green beneath when dry; pinnately veined with midrib impressed above and conspicuously raised beneath, veinlets obscure on both the surfaces; petiole 5–10 mm long, glabrate when mature, ferrugineous tomentose when immature, subterete, slightly winged. *Inflorescence* short racemose or subcorymbose, 10–20-flowered; rachis 1.5–2.5 cm long, subterete, coarsely angled, densely ferrugineous tomentose; floral bracts and bracteoles oblong, acute, 2–5 mm long and ca. 1 mm wide, ferrugineous tomentose on both the surfaces; pedicels subterete, striate, 15–24 mm long and ca. 0.5 mm in diameter, densely ferrugineous tomentose becoming glabrate. *Flowers* with the calyx 2–3 mm long, densely ferrugineous tomentose, glabrescent, the lobes 1.5–2 mm long, ovate, obtuse, marginally ciliate; corolla 15–17 mm long, the petals obovate, densely ciliate at distal tips, light pink, with darker pink "honey guides"; stamens 15–16 mm long, the filaments 13–14 mm long, densely pilose on the basal third, the anthers obconic, ca. 2 mm long; style 21–22 mm long, to 28 mm long after anthesis, glabrous; stigma capitate; ovary glabrous. *Capsule* 7–8 mm in diameter.

Befaria glauca is geographically the most widespread and morphologically the most variable species in the genus. Mansfeld & Sleumer (1935) recognized five varieties within the species and these were distinguished primarily by characters of indumentum. This ephemeral character is unusable as its facies change with the age of the plant. Therefore, the varieties of *B. glauca* based on indumentum are questionable. Without personal extensive field experience, we cannot evaluate the problem critically. The Panamanian material seemingly falls within the morphological variability of var. *coarctata* but grades into var. *glauca*.

CHIRIQUÍ: Cerro Colorado, 50 km N of San Félix on the continental divide, cloud forest, 1200–1500 m, *Mori & Dressler* 7830 (DUKE, MO), 7833 (DUKE, MO). N of San Félix at



FIGURE 4. *Befaria glauca* Humboldt & Bonpland. Habit ($\times \frac{3}{5}$). [After Mori & Dressler 7833 (MO).]

Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine road along continental divide, 5000–5500 ft, *Mori & Kallunki 5811* (DUKE, MO). VERAGUAS: Orillas de Río San Juan, region de La Yeguada, 645 m, *Correa 1908* (MO).

5. CAVENDISHIA

Cavendishia Lindl., Bot. Reg. 21: sub *pl. 1791*. 1836. TYPE: *C. nobilis* Lindley.

?*Chupalon* Adans., Fam. Pl. 2: 164. 1763.

Socratesia Klotzsch, Linnaea 24: 22. 1851. TYPE: *S. melastomoides* Klotzsch.

Polyboea Klotzsch, Linnaea 24: 24. 1851.

Proclesia Klotzsch, Linnaea 24: 32. 1851.

Erect *shrubs*, evergreen, epiphytic or terrestrial; bark thin, cracking longitudinally. *Leaves* alternate, simple, estipulate, plinerved or pinnate, coriaceous, marginally entire and revolute, both surfaces usually with multicellular, reddish or blackish, slightly sunken, glandular trichomes to 0.2 mm long, if glabrescent appearing punctate. *Inflorescence* axillary, racemose or subfasciculate, usually solitary, encircled at the base by a progression of bracts, the smallest bracts minute and triangular, the largest conforming to the shape and size of the individual floral bracts, the inflorescence bracts few to numerous, imbricate, coriaceous, smooth or minutely striate or muricate, marginally scarious and usually minutely glandular fimbriate; floral bracts solitary at base of pedicel, usually large and showy; pedicels cylindric, bibracteolate near the base or rarely midway up the pedicel; bracteoles chartaceous or coriaceous. *Flowers* with the hypanthium articulate at the pedicel, constricted at the base of the limb, the tube basally expanded or not, fused with the ovary wall, the limb erect or spreading, free from the ovary wall, 5-lobed; corolla tubular, usually carnose when fresh, 5-lobed, the lobes valvate or conduplicate valvate, usually flaring at anthesis; stamens 10, subequal or rarely unequal, subequalling the corolla, the filaments ligulate, usually distinct, rarely slightly coherent at the extreme base at anthesis, alternately unequal, the anthers alternately unequal, the thecae smooth or slightly granular, the tubules about the same width as the thecae and about twice as long, dehiscent by introrse, elongate clefts; ovary inferior, 5-locular, surmounted by a flat or cupuliform, nectariferous disc, the style filiform, straight or sigmoid, usually glabrous, the stigma minutely 5-lobed, truncate but slightly flaring at anthesis. *Fruit* a juicy, spherical, dark blue black berry; *seeds* many, minute, 0.5–1 mm long, the testa ruminant.

Cavendishia may be easily recognized by usually large, brightly colored floral bracts and by stamens with alternately unequal filaments and anthers.

Cavendishia is a neotropical genus of epiphytic and terrestrial shrubs with approximately 150 species. They are distributed from the Mexican state of Oaxaca south through montane Central America to Bolivia, and as far east as Surinam. The greatest concentration of species occurs in Colombia where approximately 70 species have been recognized. In Central America the genus is most abundant in Panama and Costa Rica where all of the 30 species recognized occur. Most species have narrow distributional ranges; many are restricted to single mountain ranges or to one particular peak. *Cavendishia crassifolia* has

the greatest geographic distribution of the Central American species ranging from Mexico to Panama. *Cavendishia callista* is found in Guatemala and again in Costa Rica and Panama.

Literature:

Luteyn, J. L. 1975. The genus *Cavendishia* (Vacciniaceae) in Costa Rica. *Brenesia* 6: 9–18.

———. 1976. A revision of the genus *Cavendishia* (Vacciniaceae) in Mexico and Central America. *Mem. New York Bot. Gard.* 28(3): 1–138.

- a. Leaves sessile to subsessile, amplexicaul with strongly cordate bases; calyx lobes imbricate 7. *C. complectens*
- aa. Leaves subsessile to long petiolate, never amplexicaul, and with variously shaped but never strongly cordate bases; calyx lobes not imbricate, or if basally contiguous then the leaves long petiolate.
 - b. Calyx tube usually conspicuously enlarged basally or with a wide spreading basal rim, if inconspicuously enlarged then with globular glands; calyx lobes and bracteoles marginally, apically, or completely glandular-callose thickened or with intermittent stout, oblong glandular thickenings (*C. quercina*), the lobes never glandular fimbriate, the bracteoles rarely glandular fimbriate and if with glandular fimbriae then the calyx and corolla pilose and the leaves less than 7 cm long (bracteoles eglandular in *C. santafeënsis*); calyx lobes erect after anthesis.
 - c. Leaves apically rounded, obtuse, if acute then the leaves usually less than 7 cm long; corolla 15 mm long or less; calyx sinuses usually ciliate; calyx lobes with several, small, intermittent, stout glandular thickenings which sometimes coalesce distally to form short oblong glandular thickenings 19. *C. quercina*
 - cc. Leaves apically acuminate to caudate acuminate, if acute then leaves mostly more than 7 cm long; corolla usually 15 mm long or more; calyx sinuses glabrous; calyx lobes completely callose thickened, or with distinct thickenings running the length of the margin.
 - d. Plants with globular, peltate, red glands to 0.7 mm in diameter on calyx tubes, floral bract margins, bracteole margins, pedicels, and rachises; leaves with scattered globular glands 0.1–0.2 mm in diameter along the upper surface and the margin, these caducous leaving a reddish or blackish, papillate scar; calyx tube little or not enlarged.
 - e. Leaves linear lanceolate to linear elliptic, about 9 times as long as broad, usually without globular glands at maturity; bracteoles ca. 25 mm long, located just below the calyx; Bocas del Toro and Veraguas (Atlantic slope) Provinces 17. *C. pseudostenophylla*
 - ee. Leaves elliptic, lance elliptic to ovate lanceolate, less than 4 times as long as broad, with globular glands at maturity; bracteoles less than 5 mm long, located at the base of the pedicel; Chiriquí Province.
 - f. Leaves less than 10 cm long and 4 cm wide, apically caudate acuminate; rachis less than 5 cm long, ca. 1 mm in diameter at its base, with 6–9(–11) flowers; floral bracts less than 30 mm long; bracteoles linear; pedicels less than 10 mm long; calyx 3.5–4.5 mm long, the tube surface not obscured by globular glands, the lobes entirely callose thickened; corolla less than 25 mm long; style less than 25 mm long 6. *C. chiriquiensis*
 - ff. Leaves greater than 10 cm long, 4 cm or more wide, apically acuminate; rachis greater than 8 cm long, ca. 5 mm in diameter at its base, with 11–21 flowers; floral bracts 30 mm long or longer; bracteoles ovate to lanceolate; pedicels 10 mm or more long; calyx 4–6 mm long, the tube surface obscured

- by globular glands, the lobes marginally callose thickened; corolla 25 mm or more long; style 25 mm long or more ----- 16. *C. panamensis*
- dd. Plants without globular, peltate, red glands; leaves without globular glands; calyx tube conspicuously basally enlarged.
- g. Calyx lobes with oblong, callose-thickened glands the entire length of each margin; bracteoles 3 cm or more long; Veraguas Province ----- 21. *C. santafeënsis*
- gg. Calyx lobes completely glandular callose thickened over the entire surface, not just marginally; bracteoles less than 1 cm long.
- h. Leaves linear to elliptic lanceolate, 5–6 times as long as broad, pinnately veined, marginally strongly revolute; floral bracts marginally callose thickened for the distal $\frac{2}{3}$; bracteoles continuous with the pedicels ----- 22. *C. stenophylla*
- hh. Leaves variously shaped but never linear, less than 5 times as long as broad, plinerved, marginally nearly flat; floral bracts marginally eglandular; bracteoles articulated with the pedicels.
- i. Floral bracts apically acute or rounded, never emarginate; rachis elongate, 3–12(–20) cm long, rarely shorter (and then floral bracts 6–10 mm long).
- j. Corolla pubescent; floral bracts (15–)25–40(–50) mm long.
- k. Corolla densely sericeous, white; rachis (4–)6–12(20) cm long with 20–35 flowers; petioles densely pilose to glabrate; Veraguas, Coclé, and Panamá Provinces ----- 4. *C. callista*
- kk. Corolla short pilose, purple; rachis 3–6(–9) cm long with (7–)11–16(–20) flowers; petioles glabrous even when young; Chiriquí Province ----- 2. *C. atrovioacea*
- jj. Corolla glabrous; floral bracts 6–20 mm long.
- l. Corolla 18–20 mm long, lobes callose thickened; bracteoles lanceolate; floral bracts 15–20 mm long; Darién Province ----- 15. *C. morii*
- ll. Corolla 28–32 mm long, lobes not callose thickened; bracteoles broadly ovate to hemispheric; floral bracts 6–10 mm long; Chiriquí Province ----- 14. *C. melastomoides* var. *coloradensis*
- ii. Floral bracts apically rounded and usually noticeably emarginate; rachis short (0.3–)0.6–2(–3.5) cm long.
- m. Corolla 27–43 mm long; stamens 24.5 mm long or more; style more than 30 mm long; floral bracts (2–)3–6(–7) cm long, dark red in bud but turning pink or pale purplish red at anthesis; calyx 7–13 mm long, the limb including the lobes (4–)5–7.5(–9) mm long and cylindric to slightly spreading ----- 13. *C. megabracteata*
- mm. Corolla 20–24(–30) mm long; stamens 24.5 mm long or less; style less than 30 mm long; floral bracts 1.5–3(–4) cm long, green; calyx 5–7(–10) mm long, the limb including the lobes 2.5–4.5(–6) mm long and campanulate to cylindric ----- 23. *C. subfasciculata*
- bb. Calyx tube basally rounded, truncate, or with a narrow rim, never conspicuously enlarged, the rim never flaring, never with globular glands on the surface of the tube; calyx lobes and bracteoles usually with marginal, caducous glandular fimbriae to 0.2 mm long, never callose thickened (calyx lobes eglandular in *C. darienensis*; bracteoles eglandular in *C. fusiformis*); calyx lobes connivent or erect after anthesis.
- n. Calyx limb and floral bracts conspicuously striate; bracteoles striate and

- 5–20 mm long, if smooth then more than 20 mm long; floral bracts persistent in fruit.
- o. Bracteoles smooth, more than 20 mm long, apically rounded and emarginate; corolla more than 30 mm long; stamens about $\frac{1}{3}$ as long as the corolla; calyx limb more than 8 mm long; Darién Province 10. *C. fusiformis*
 - oo. Bracteoles striate, less than 20 mm long, apically rounded, acute or acuminate but never emarginate; corolla less than 20 mm long; stamens about as long as the corolla; calyx limb less than 8 mm long.
 - p. Leaves pinnately veined; floral bracts 13 mm long or less, obovate to semiorbicular; bracteoles 9 mm long or less; corolla 10 mm long or less 3. *C. axillaris*
 - pp. Leaves plinerved; floral bracts 13 mm long or longer, lanceolate to elliptic or ovate elliptic, rarely obovate or semiorbicular; bracteoles usually more than 10 mm long; corolla more than 10 mm long.
 - q. Twigs, leaves, rachises, pedicels, floral bracts, bracteoles, calyces, and corollas short pubescent; rachis more than 8 cm long; floral bracts lanceolate, apically long acuminate; calyx lobes marginally eglandular; corollas nonstriate; Darién Province 9. *C. darienensis*
 - qq. Plants glabrous throughout; rachis less than 5 cm long; floral bracts elliptic, ovate elliptic, obovate, or rarely semiorbicular, apically acute; calyx lobes marginally glandular fimbriate; corollas conspicuously striate; Coclé and Panamá provinces 1. *C. allenii*
 - nn. Calyx limb and floral bracts never striate; bracteoles smooth, never striate, rarely more than 5 mm long; floral bracts caducous soon after anthesis.
 - r. Leaves apically obtuse or rounded, usually less than 6 cm long; calyx lobes erect after anthesis; rachis subfasciculate, less than 1 cm long with 3–6(–7) flowers; pedicels 1.5–2(–5) mm long 5. *C. capitulata*
 - rr. Leaves apically acuminate or sharply acute, usually greater than 6 cm long; calyx lobes connivent or erect after anthesis; rachis elongate, usually more than 1 cm long with 6 or more flowers; pedicels more than 3 mm long.
 - s. Calyx 9–14 mm long.
 - t. Leaves glabrous, very thick coriaceous, the margins so tightly revolute as to be obscured from view; calyx glabrous; style 10–11 mm long; plants reportedly with odor of wintergreen; Cerro Jefe, Panamá Province 20. *C. revoluta*
 - tt. Leaves pilose on both surfaces, membranaceous to coriaceous but not conspicuously thickened, the margins only slightly revolute; calyx densely pilose; style ca. 21 mm long; plants lacking the odor of wintergreen; Cerro Tacarcuna, Darién Province 11. *C. gentryi*
 - ss. Calyx less than 9 mm long.
 - u. Corolla 8–10(–12) mm long; floral bracts 7–13 mm long; rachis 4–15(–20) cm long; Darién Province 12. *C. laurifolia*
 - uu. Corolla (12–)15–25 mm long; floral bracts (11–)17–40 mm long; rachis 1–5(–8) cm long.
 - v. Calyx pubescence of densely matted trichomes; plants including mature berry persistently short, white pilose; corollas white or white with a pinkish hue; floral bracts pale green often with a pinkish hue; Chiriquí Province 18. *C. pubescens*
 - vv. Calyx glabrous or trichomes usually sparse and short, never densely matted; plants glabrous or variously pubescent but mature berry always glabrous; corollas pink to red with white tips; floral bracts red; Chiriquí, Veraguas, Coclé, and Panamá provinces 8. *C. crassifolia*

1. **Cavendishia allenii** A. C. Smith, Ann. Missouri Bot. Gard. 28: 445. 1941.
TYPE: Panama; Coclé, N of El Valle de Antón, 1,000 m, *Allen 2471* (A, holotype; photo of type, DUKE, NY).

Epiphytic *shrub* to 1 m tall, glabrous throughout; stem base to 1.5 cm in diameter; branches terete or subterete, smooth or somewhat striate when immature, reddish brown, bark reddish or grayish brown. *Leaves* elliptic or ovate elliptic, (3.5–)5–11.5 cm long, 2–7 cm wide, basally rounded or somewhat subcordate, apically acute or broadly obtuse, dull olive brown and shining when dry; inconspicuously 3–5(–7)-plinerved, the midrib impressed above, raised beneath, prominent on both the surfaces, the primary lateral nerves thin, raised on both the surfaces, far removed from the midrib, the secondary nerves thick, raised and conspicuous above causing the leaf to appear pinnately veined; petioles terete, rugose, 1–4 mm long, 1–3 mm in diameter. *Inflorescences* tightly congested racemes, 8–16 flowered basally encircled by striate bracts, the rachis bluntly angled, smooth or striate, often muricate, 1.5–4 cm long, ca. 2 mm in diameter at anthesis, elongating to 6 cm in the fruit; floral bracts conspicuously striate, concave, elliptic, ovate elliptic or obovate, rarely semiorbicular, basally rounded to truncate, slightly auriculate, apically acute, sometimes broadly so, the margins often so tightly revolute that the bracts appear sharply acuminate, (13–)15–20 mm long (6–)8–12(–18) mm wide, rose or salmon pink or pale green with a pinkish hue, marginally glandular fimbriate, the fimbriae early caducous, the bracts persisting as the berry matures; pedicels subterete, 1–1.5(–3) mm long, 1–1.5 mm in diameter; bracteoles striate, concave basally, ovate lanceolate or oblong, apically rounded or acute, 11–13(–17) mm long, (3–)5–7 mm broad, marginally glandular fimbriate, tightly imbricate in bud, completely enclosing the calyx, often persistent in fruit. *Flowers* with the calyx 8–12(–15) mm long, pink, the tube barrel-shaped or globose at anthesis, smooth or slightly rugose, not enlarged, 2–4.5(–5) mm long, 2–4 mm in diameter, the limb cylindric, striate, (3.5–)5–7(–9) mm long including the lobes, the lobes triangular or nearly oblong, acute, or apiculate, 1.5–2 mm long and broad, erect after anthesis, marginally glandular fimbriate and slightly scarious, the sinus acute to obtuse, corolla tubular, slightly wider medially, conspicuously striate, 11.5–16 mm long, 3.5–4 mm in diameter, pale green with a yellow tip, the lobes oblong, bluntly acute, 2–3.5 mm long, slightly thickened at the tip, erect at anthesis; stamens 9.5–13 mm long, the filaments coherent at base, distally pubescent, alternately 2.5–4 mm, 3.5–5 mm long, the anthers including the tubules alternately 7–10.5 mm and 8.5–12 mm long, the thecae 2–3.5 mm long; style 11.5–14.5 mm long. *Berry* 15 mm in diameter.

Cavendishia allenii is the only *Cavendishia* in Central America with a corolla that is conspicuously nerved or striate and pale green with a yellow tip. It is endemic to central Panama, being found between 200–1,000 m elevation. Its relationship to *C. darienensis* is discussed under that species.

COCLÉ: El Valle de Antón, 600 m, *Allen 2068* (MO); *Allen 2278* (GH, MO, US). El Valle, 800 m, *Allen 2308* (MO). Trail to Las Minas, N of El Valle de Antón, 1000 m, *Allen 2471* (A). N of El Valle de Antón, La Mesa, 1000 m, *Allen 2834* (A); *Allen 2897* (A, MO).

Ridge of Loma del Tigre, 865 m, *Allen* 4481 (MO). Cloud forest on slopes of Cerro Pílon near El Valle, 700–900 m, *Duke* 12162(2) (MO). Cerro Pílon, 890 m, *Dwyer* 8328 (MO). Mountains beyond La Pintada, 400–600 m, *Hunter & Allen* 572 (F, G, MO, S). Trail beyond La Mesa towards Los Llanos, 800–860 m, *Luteyn* 3173 (DUKE, NY); *Luteyn* 4100 (DUKE, MICH, NY). COLÓN: E of Santa Rita ridge, *Correa* 646 (MO). Santa Rita Ridge road, 4 mi from Transisthmian Highway, 500 m, *Gentry et al.* 8861 (NY). PANAMÁ: 19 km along Cartí road, 500 m, *Busey* 885 (DUKE). Cerro Jefe, 0.5 km S of summit, *Busey & Croat* 266 (MO). La Eneida, *Dressler* 3229 (MO). Cerro Jefe, *Duke* 9427 (MO); *Dwyer et al.* 7299 (MO). Cerro Jefe to La Eneida, 650–890 m, *Dwyer et al.* 8224 (MO). Cerro Jefe, Altos de Pacora, 800–900 m, *Gentry & Mori* 13431 (NY). 10–16 km from Panamerican Highway on El Llano-Cartí-Tupile road, *Kennedy* 2507; *Kennedy et al.* 2415; *Liesner* 1149, 1322 (all MO); *Luteyn & Wilbur* 4664 (DUKE, MO); *Luteyn & Wilbur* 4682 (DUKE). 5–10 km NE Altos de Pacora, 750 m, *Mori & Kallunki* 4954 (NY). 10–12 km N of Inter-American Hwy along El Llano-Cartí-Tupile road, ca. 500 m, *Wilbur & Luteyn* 19504 (DUKE). Beyond Cerro Azul, ca. 5.5 mi on road to La Eneida, 830–925 m, *Wilbur & Teeri* 13630 (DUKE). Trail off Cerro Jefe road, 0.4 km beyond turnoff to Altos de Pacora, *Witherspoon & Witherspoon* 8586 (MO, NY).

2. ***Cavendishia atrovioacea*** Luteyn, *Brittonia* 28: 49. 1976. TYPE: Panama; *Luteyn* 3045 (DUKE, holotype; F, GH, LL, MICH, MO, NY, PMA, UC, US, isotypes).

Epiphytic *shrub* 1–3 m tall, stem base to 2.5 cm in diameter; mature branches terete to subterete, smooth or minutely striate, glabrous, 6–7 mm in diameter, often red dorsally and green ventrally when fresh; bark brown, but drying yellowish, grayish, or reddish brown, the immature branches and twigs of the new growth subterete to bluntly angled, minutely striate, glabrous, reddish brown when dry. *Leaves* lanceolate to lance elliptic, rarely oblanceolate or ovate, (3–) 8–12(–18) cm long and 1–4(–6) cm broad, basally rounded, obtuse, cuneate or rarely subtruncate, apically acuminate, olive tan or silvery green when dry, glabrous or rarely with a few hairs at the base of the midrib on the upper surface; (3–) 5(–7)-plinerved, veins impressed above or rarely veinlets and the outer pair of lateral veins raised, the midrib raised and prominent beneath, the lateral veins raised, prominent to obscure beneath, the veinlets slightly raised, usually obscure beneath; petioles terete or often flattened adaxially, rugose, (4–) 6–15 mm long, (0.7–) 1–1.5(–2.5) mm in diameter, glabrous, green suffused with maroon, drying reddish brown. *Inflorescence* (7–) 11–16(–20) flowered, cylindric to fusiform in bud, rachis long tapering, cylindric, bluntly angled, minutely striate, viscid, glabrous, 3–6(–9) cm long, 2–5 mm in diameter, pink to pinkish white when fresh; floral bracts rarely translucent when dry, glabrous, smooth or reddish papillate abaxially, oblong to oblanceolate, rarely obovate or somewhat spatulate, basally narrowed and truncate, apically rounded to acute, (2–) 2.5–4(–5) cm long, 1–2 cm broad, deep violet or maroonish purple, often appearing black; pedicels swollen distally, striate or ribbed, glabrous, (6–) 9–13(–16) mm long, 0.7–(–1.5) mm in diameter, pink to pinkish white when fresh; bracteoles lanceolate to linear lanceolate, rarely ovate, 2–4(–5.5) mm long, 0.6–1(–2) mm broad, basally slightly auriculate, apically acuminate and glandularly callose thickened in the distal third, purplish pink when fresh. *Flowers* with the calyx glabrous, (6–) 7–11(–13.5) mm long, the tube cylindric, coarsely ribbed, (2–) 2.5–4(–5.5) mm long, basally (2.5–) 3–6(–6.5) mm in diameter, basally enlarged and deeply lobed, the lobes straight or flaring outward and extending well be-

low the basal articulation, pinkish red to purplish at anthesis turning pale green post anthesis, the limb cylindric or somewhat spreading, weakly ribbed or minutely papillate, (3.5–)5–8 mm long including the lobes, pinkish red, the lobes triangular, 1–2(–2.5) mm long, and 2–2.5 mm broad, erect after anthesis, glandular callose thickened without, dark reddish purple or green; sinus obtuse to broadly rounded; corolla slightly constricted basally, narrowed to the throat, sometimes translucent when dry, (25–)30–38(–45) mm long, 5–8 mm in diameter, pilose with short, white trichomes, the tube whitish purple at the constricted base, purple to dark purple above, the limb and the lobes pale purple, the lobes oblong, obtuse, 1.5–2 mm long, strongly reflexed at anthesis; stamens 24–39 mm long, the filaments glabrate or moderately pilose distally, alternately 3.5–6 mm and 7.5–14.5 mm long, white, the anthers including tubules alternately 16.5–27.5 mm and 22.5–35.5 mm long, orange, the thecae 6–13.5 mm long; style 35–46 mm long. *Berry* not seen.

Cavendishia atrovioleacea can be recognized by the large, violet to very dark maroonish purple floral bracts which are striking in the living condition. This character along with a purple corolla, greenish to reddish green calyx, and many flowered inflorescences combine to make it one of the most beautiful species in the Chiriquí highlands. This species is a near Panamanian endemic having been collected elsewhere only once on the southwest slopes of Cerro Pando along the border between Panama and Costa Rica. *Cavendishia atrovioleacea* seems most closely related to the widespread *C. callista*.

CHIRIQUÍ: NW side of Cerro Punta, Las Nubes, 2000–2400 m, *Almeda* 1535 (DUKE, NY); *Croat* 10459, 22414 (both MO), 26465 (MO, NY). Slopes of Cerro Punta, 2000 m, *Gentry* 5878 (MO). NW side of Cerro Punta, Las Nubes, 2000–2400 m, *Luteyn* 3045 (DUKE, F, GH, LL, MICH, MO, NY, PMA, UC, US), 3804 (DUKE, F, MICH, MO, NY, US). Bajo Chorro Trail, 2360–2500 m, *Luteyn* 3059, 3814 (both DUKE). Monte Lirio, 1300–1900 m, *Seibert* 176 (US). NW side of Cerro Punta, Las Nubes, 2000–2400 m, *Utley et al.* 244 (DUKE, NY). Valley of the upper Río Chiriquí Viejo, 1300–2000 m, *White & White* 23 (MO). NW side of Cerro Punta, Las Nubes, 2000–2400 m, *Wilbur & Almeda* 17072 (DUKE, F, GH, MO, NY, US); *Wilbur & Teeri* 13202 (DUKE). Along Río Chiriquí Viejo, ridge of Cerro Respinga, 2160 m, *Wilbur & Teeri* 13117 (DUKE). NW side of Cerro Punta, Las Nubes, 2000–2400 m, *Wilbur et al.* 11954 (DUKE). Valley of the upper Río Chiriquí Viejo, 1300–2000 m, *Wilbur et al.* 13036 (DUKE, F, MO, NY).

3. ***Cavendishia axillaris*** A. C. Smith, Contr. U. S. Natl. Herb. 28: 493. 1932. TYPE: Colombia; Bolívar, 2,300–2,700 m, *Pennell* 4375 (NY, holotype; photo of type, DUKE).

C. gaultherioides A. C. Smith, Ann. Missouri Bot. Gard. 28: 444. 1941. TYPE: Panama; Coclé, La Mesa, N of El Valle de Antón, 1000 m, *Allen* 2375 (A, holotype; photo of holotype, DUKE, NY; MO, isotype).

Terrestrial or epiphytic *shrubs*, 0.5–1.5(–3) m tall, glabrous throughout when mature; stem base 1–2.5 cm in diameter; mature branches often arching, terete to bluntly angled, smooth or striate; bark often reddish above and brown to grayish brown beneath; immature branches and twigs of new growth terete or flattened, densely puberulent, glabrescent. *Leaves* ovate, obovate, elliptic or suborbicular, 4.5–10.5(–17) cm long, (2.5–)4–11 cm broad, basally cuneate, obtuse, rounded or subcordate and then often slightly amplexicaul, apically obtuse

or rounded, grayish to brownish green above and tan to olive green beneath when dry, pinnately veined, the midrib elevated on both the surfaces, the proximal $\frac{1}{3}$ conspicuously thickened, 3–5 times thicker than the narrowed and impressed distal portion, the lateral nerves arcuate, anastomosing near the margin, impressed above, sometimes strongly so, raised and prominent beneath, the leaves hence frequently bullate, the veinlets impressed or slightly raised above, elevated beneath, newly unfolding leaves puberulent but later glabrate; petioles subterete, striate or rugose, 1.5–3(–5) mm long, 2.5–3.5(–4.5) mm in diameter, dark reddish brown. *Inflorescences* solitary racemes or rarely 2–5 per axil, tightly racemose, the floral internodes ca. 1 mm long, (5–)9–15(–47) flowered, capitate or cylindric at anthesis, encircled at the base by striate bracts, the rachis terete or bluntly angled, 1–2(–8) cm long, the floral nodes swollen; floral bracts smooth or muricate, striate when dry with conspicuously thickened, dichotomously branching veins, obovate to semiorbicular, basally truncate, apically rounded or acute, the apex usually splitting deeply, 7–10(13) mm long, (5.5–)8–11(–13) mm broad, marginally scarious and densely glandular fimbriate, concave, tightly appressed to and concealing the calyx and the lower portion of the corolla at anthesis, often persistent until after the berry has matured; pink to dark rose red; pedicels to 1 mm long, 1 mm in diameter, rarely with few cartilaginous teeth distally; bracteoles smooth or muricate but conspicuously striate when dry, elliptic oblong, basally truncate, apically rounded, (5–)7–9 mm long, (2–)4–6 mm wide, marginally scarious and densely glandular fimbriate, concave and strongly keeled, rarely flat, imbricate and completely enveloping the perianth in bud, tightly appressed to the calyx at anthesis, pink to dark rose red. *Flowers* with the calyx (4.5–)6–7.5 mm long, the tube cylindric, smooth to rugose, non-expanded basally (1.5–)2.5–3 mm long, 2.5 mm in diameter, pink to pale green, the limb spreading to campanulate, conspicuously striate within and without when dry, (2.5–)3.5–4(–5) mm long including the lobes, pale green, the lobes ovate to triangular, rarely oblong, acute, 1–2 mm long and 1.5–3 mm wide, erect after anthesis, the margins glandular fimbriate and occasionally slightly imbricate at the base, pale green and occasionally marginally pink, the sinuses acute or narrowly obtuse; corolla cylindric or slightly bottleshaped, narrowed at the throat, (6.5–)9–10 mm long, 3.5–4(–6) mm in diameter, often glandular fimbriate distally, white to pale green in the basal $\frac{1}{3}$, green to yellowish green in median $\frac{2}{3}$, the limb and the lobes pale green, the lobes oblong to narrowly triangular, obtuse, 1–2 mm long; stamens 6–8.5 mm long, the filaments short puberulent distally, alternately 1.5–2.5 mm and 2.5–3.5 mm long, the anthers including tubules alternately 4–6 mm and 5–6.5 mm long, the thecae 1.5–2.5 mm long; style 8–9 mm long. *Berry* 9–10 mm in diameter.

Cavendishia axillaris ranges from Costa Rica and Panama south into Colombia and adjacent Ecuador. In Central America it is generally found between 700–1,500 meters. It is well characterized by its pinnately veined, subsessile leaves, compact inflorescences, its conspicuously nerved floral bracts and bracteoles which are tightly appressed to the calyx, and by its small flowers. Numerous Central American collections have been misidentified as *C. complectens*. Together they share pinnately veined leaves and compact inflorescence, although

the rachis of *C. complectens* may lengthen considerably after anthesis. They are most easily separated by the fact that the leaves of *C. complectens* are strongly amplexicaul and the calyx lobes are reniform and broadly imbricate, whereas in *C. axillaris* the leaves are never amplexicaul, the calyx lobes are triangular to ovate and are only rarely imbricate at the very base.

CHIRIQUÍ: Between Pinola and Quebrada Hondo, Chiriquí Trail, *Kirkbride & Duke* 879 (MO). COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen* 2170 (A); *Allen* 2329 (A, MO). La Mesa, N of El Valle de Antón, *Allen* 2375 (A, MO); *Allen* 2736, 2787 (both A). Hills N of El Valle de Antón, 1000 m, *Allen* 3559 (G, MO). 39 km from Interamerican Highway along El Valle dirt road, *Correa* 327 (MO). La Mesa, N of El Valle de Antón, *Croat* 14393 (MO, NY). Along road past Furlong's finca, due N of Cerro Pilon, 880 m, *Croat* 37549 (NY). Cloud forest on Cerro Pilon, 700–900 m, *Duke* 12175 (MO). 9 km from El Valle market beyond Sr. Furlong's finca, *Kennedy et al.* 3188 (MO). N of El Valle, beyond La Mesa towards Los Llano, 800–850, *Luteyn* 3157, 4112 (both DUKE); *Luteyn & Kennedy* 1689 (DUKE). Roadside, La Mesa, 4 km N of El Valle, 875 m, *Nee & Dwyer* 9169 (NY). Cerro Pilon above El Valle, 620 m, *Porter et al.* 4467, 4639 (both MO). La Mesa, N of El Valle de Antón, *Wilbur et al.* 11116 (DUKE). DARIÉN: Cerro Tacarcuna massif between summit camp on westernmost ridge and Pico Tacarcuna, 1650–1800 m, *Gentry, Leon & L. Forero* 16916 (NY). Elfin forest at top of W peak of Cerro Tacarcuna massif, 1800–1850 m, *Gentry & Mori* 13979 (MO, NY). VERAGUAS: Santa Fé, slopes of Cerro Tute, 925 m, *Allen* 4343 (G, MO, US). Road between Escuela Agrícola Alto Piedra and Río Dos Bocas, 730–770 m, *Croat* 25913 (MO). 20 km NW Santa Fé, 650–800 m, *Kennedy & Dressler* 3420 (NY). Road past Escuela Agrícola Alto Piedra on Pacific side, 800–1000 m, *Liesner* 862 (MO); *Luteyn & Wilbur* 4578 (DUKE, F, MO, NY). NW of Santa Fé, 1–4.2 km from Escuela Agrícola Alto Piedra, *Mori & Kallunki* 4026 (WIS), 4827 (NY). 6–7 km W of Santa Fé, road past agricultural school, *Nee* 9714 (NY). Along first branch of Río Santa Maria by road from Santa Fé, *Witherspoon & Dressler* 8922 (MO, NY).

4. ***Cavendishia callista*** Donnell Smith, Bot. Gaz. (Crawfordsville) 20: 5. 1895. TYPE: Guatemala; Alta Verapaz, between Cobán and Samac, 1,400 m, *Tuerckheim* 941 (US, lectotype; photo of lectotype DUKE, NY; F, G, GH, NY, islectotypes).

C. longiflora Donnell Smith, Bot. Gaz. (Crawfordsville) 37: 420. 1904. TYPE: Costa Rica; San José, Alto de La Palma, *Tonduz* 7391 (US, lectotype; photo of lectotype, DUKE; BM, F, G, GH, NY, US, islectotypes).

C. bullata A. C. Smith & Standley, Contr. U.S. Natl. Herb. 28: 453. 1932. TYPE: Costa Rica; Cartago, Naranjo, *Stork* 1789 (F, holotype; photo of holotype, DUKE, NY; G-fragments from holotype; MICH, isotype).

Epiphytic and terrestrial *shrubs*, 1.5–3 m tall; stem base ca. 2.5–5 cm in diameter; mature branches and twigs of new growth bluntly angled to terete, often glaucous, glabrous to densely pilose, often glabrescent, the trichomes tan to yellowish and 0.5–2 mm long, bark brown to reddish brown. *Leaves* ovate, lanceolate, elliptic, oblong, rarely obovate, (5–)7–26(–32) cm long, (1–)2–10(–13) cm wide, basally obtuse, rounded or truncate, often slightly cordate apically acute to long acuminate sometimes abruptly short acuminate, tan, olive brown, or reddish brown when dry, glabrous to moderately short pubescent on the lamina above, glabrate to densely pubescent beneath especially along the nerves; (3–)5(–9)-plinerved with the midrib and the lateral nerves shallowly to deeply impressed above, raised and conspicuous beneath, the veinlets usually slightly elevated on both the surfaces but secondary lateral nerves and veinlets often deeply impressed above giving the lamina a strikingly bullate appearance; petioles subterete, rugose, (4–)6–16(–22) mm long, (1–)2–3(–5) mm in diameter,

glabrous to densely pilose with trichomes to 1.5 mm long. *Inflorescence* viscid, 20–35(–52) flowered, encircled at the base by bracts, rachis bluntly angled, longitudinally ribbed, glabrous or infrequently densely sericeous, 4–12(–20) cm long, 4–6(–10) mm in diameter, rose colored but drying yellowish to orangish brown, rarely with minute, reddish, clavate glands especially at the base of the floral bracts; floral bracts pink, smooth or muricate, glabrous, oblong, obovate or oblanceolate, basally narrowed and truncate, apically rounded to acute, the tips rarely reflexed, (1.5–)2–5(–6) cm long, 1–2.5(–3.5) cm broad; pedicels smooth or rugose, usually longitudinally ribbed, usually swollen at both ends, glabrous or infrequently densely sericeous, 6–15(–20) mm long, 0.5–1.5(–2) mm in diameter, rarely with sessile, reddish glands or cartilaginous teeth at the apex; bracteoles glabrous, infrequently conspicuously nerved, ovate lanceolate, basally somewhat auriculate clasping, 1–5(–7) mm long, 1–2(–3.5) mm wide, apically glandular callose thickened, rarely callose thickened for nearly the entire length. *Flowers* with the calyx glabrous or infrequently densely pilose, 5–9(–11) mm long, viscid, the tube cylindric, coarsely ribbed, rugose, often muricate, (1.5–)2–4(–5.5) mm long, strongly expanded basally, pinkish green, at anthesis becoming green, the limb cylindric or spreading, often striate, 3.5–6(–8) mm long including the lobes, dark rose at anthesis becoming pale rose to pink, the lobes triangular, 1–2.5(–4) mm long, 2–3 mm broad, erect after anthesis, usually completely glandular callose thickened, green to brownish green when fresh, the sinus obtuse to broadly acute; corolla narrowed to the throat, viscid, 1.5–3.5(–4) cm long, 4–8 mm in diameter, densely sericeous or rarely glabrous externally, moderately pilose or rarely glabrous within with translucent trichomes 0.5–1 mm long, the tube white or with a pinkish hue basally, the lobes triangular, 1–3 mm long, 2–3 mm wide, reflexed at anthesis, white with purple margins; stamens (13–)20–34 mm long, the filaments alternately (1.5–)3.5–4.5(–6) mm and (4.5–)8–12 mm long, short pilose distally, white to pink, the anthers including the tubules alternately (8.5–)15–26 mm and (11–)27–32 mm long, the tubules purplish orange, the thecae 5–20 mm long, orange; style (17–)20–35(–40) mm long, green. *Mature berry* not seen.

Cavendishia callista is distinguished by rose pink floral bracts, and densely sericeous, white corollas which have purple margined lobes. The species is quite variable with respect to leaf size and shape, texture, degree of bullateness and pubescence, as well as pubescence of the twigs and other vegetative organs. This species is known from Guatemala, Costa Rica and Panama.

COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen* 2207 (MO), 3598 (F, G, MO, US). La Mesa above El Valle, 800 m, *Croat* 25397 (MO). Along road past Furlong's Finca, N of Cerro Pilón, 880 m, *Croat* 37570 (MO, NY). El Valle, *Dwyer* 1944 (MO). Cerro Gaital Caracoral, 1000 m, *Dwyer & Correa* 8937 (NY). Cerro Pilón, *Dwyer & Lallathin* 8656 (MO). La Mesa, above El Valle, 800 m, *Luteyn* 3158 (DUKE, MO). Trail to Las Minas, N of El Valle, *Luteyn* 3160 (DUKE, F, GH, MO, NY). Road to La Mesa, 740–800 m, *Vaughan et al.* 612 (MO). N rim of El Valle de Antón, near Cerro Turega, 650–700 m, *Woodson & Schery* 193 (CAS, G, MO, NY, US). COLÓN: Santa Rita, *Dwyer et al.* 9013 (MO). DARIÉN: Elfin forest near top of westernmost peak of Cerro Tacarcuna massif, 1720 m, *Gentry, Leon & L. Forero* 16894 (NY). PANAMÁ: Beyond Cerro Jefe, Campo Tres, 700 m, *Croat* 27052 (MO). Cerro Jefe, 890 m, *Dwyer & Gauger* 7342 (DUKE, MO); *Luteyn* 3207, 3971 (both DUKE). Altos de Pacora beyond Cerro Azul, *Mori et al.* 6921 (MO, NY). Cerro Jefe, 890–1000 m, *Mori* 6520

(NY); *Tyson et al.* 4353 (DUKE, MO). VERAGUAS: beyond Tres Brazos River, 11 km beyond Santa Fé, 650 m, *Croat* 25626 (MO).

5. **Cavendishia capitulata** Donnell Smith, Bot. Gaz. (Crawfordsville) 25: 147. 1898. TYPE: Costa Rica; San José, La Palma, *Wercklé* 11.565 (US, holotype; CR, isotype; photo of holotype DUKE, NY).

Erect, much branched, spreading, usually epiphytic *shrub* 0.5–1.5(–2) m tall, stem base 1–3(–15) cm in diameter; mature branches terete to bluntly angled, glabrous, bark brown, rusty brown or gray to almost black; immature branches and twigs of new growth bluntly angled, glabrous or densely hirsute with spreading, white or yellowish trichomes ca. 0.5 mm long, frequently with clavate, reddish glandular fimbriae ca. 0.1 mm long. *Leaves* obovate, oblanceolate, elliptic, oblong elliptic or ovate, 1.5–3(–6) cm long, 0.5–1.5(–3) cm wide, basally cuneate or rounded, apically rounded, obtuse or rarely abruptly tapering to a blunt tip, dull green or olive to grayish brown when dry, the young leaves densely puberulent, glabrate at maturity; 3–5(–7)-plinerved, the midrib impressed or slightly raised, conspicuous above, raised and conspicuous beneath, lateral nerves slightly raised and conspicuous or plane and obscure on both surfaces, the veinlets slightly raised, conspicuous or obscure above, usually obscure beneath; petioles smooth, striate or more commonly rugose, subterete or flattened, 1–3(–5) mm long and 0.5–1 mm in diameter, puberulent, glabrescent, brown, reddish brown or blackish. *Inflorescence* fasciculate, 3–6(–7) flowered; rachis glabrous, 1–3(–7) mm long, 1–1.5 mm in diameter; floral bracts smooth or muricate, glabrous, obovate, basally narrowed, apically rounded, shallowly emarginate or rarely acute 11–14(–19) mm long, 6.5–11 mm wide, purple to reddish purple, marginally scarious and sparsely fimbriate, rarely densely ciliate, frequently with scattered, short, thick, reddish brown, glandular fimbriae along the lamina; pedicels cylindric or obconic, rugose or obscurely ribbed, sometimes bluntly angled, glabrous or sparsely pilose distally, (0.5–)1.5–2(–5) mm long 1–1.5(–2.5) mm in diameter, rarely with reddish brown, glandular, distal fimbriae; bracteoles oblong to oblong elliptic, (1–)3–6(–8.5) mm long, 1–2 mm wide, basally truncate, apically obtuse, purple, marginally scarious and densely glandular fimbriate with fimbriae to 0.8 mm long. *Flowers* with the calyx 4.5–7.5 mm long, the tube cylindric or barrel-shaped, often pentagonal in cross section, smooth or minutely rugose, 1–3 mm long, 2–3 mm in diameter, slightly enlarged with a narrow rim or collar basally, green to purple, sometimes with scattered, reddish brown, glandular fimbriae, the limb erect, somewhat spreading or campanulate, 1.5–4 mm long including the lobes, green to greenish white, the lobes triangular, obtuse to acute, 0.5–1.5 mm long, 1.5–2 mm wide, erect or somewhat connivent after anthesis, densely glandular fimbriate with fimbriae to 0.2 mm long, the sinuses broadly rounded or obtuse, rarely acute; corolla constricted basally, narrowed to the throat, 10–16 mm long, 4–5 mm in diameter, glabrous, the basal $\frac{1}{4}$ white or pale red, the middle $\frac{1}{2}$ purple or reddish purple, the distal $\frac{1}{4}$ white, the lobes white, triangular, obtuse, 1 mm long; stamens 9–14.5 mm long, the filaments glabrous or distally with scattered hairs,

alternately either 1.5–3 mm or 3–6 mm long, the anthers including tubules alternately 5.5–10 mm and 7.5–12.5 mm long, the thecae 2–3 mm long; style (9.5–)11–15.5 mm long, the stigma somewhat peltate. *Berry* 5–7 mm in diameter.

Cavendishia capitulata ranges from Costa Rica to Panama and is found between 350–2,700 m elevation. It is distinctive despite the fact that the leaves are quite variable with respect to length and width. In Costa Rica and western Panama the leaves are usually narrowly oblong or elliptic, 2–2.5 cm long, 0.5–1 cm broad, and both the apex and the base are rounded, but the leaves may be obovate oblanceolate with cuneate bases. In central and eastern Panama, from Santa Fé de Veraguas to the Province of Darién, the leaves are usually much longer and broader, averaging 2.5–5.5 cm long and 1–2.5 cm broad. However, in floral characters these geographical variants are similar in all respects, and infraspecific recognition of these variants is not warranted.

BOCAS DEL TORO: Between Criollo and Quebrada Higueron on Chiriquí Trail, *Kirkbride & Duke* 778 (MO, NY). BOCAS DEL TORO-CHIRIQUÍ border: Cerro Colorado copper mining road, N of San Félix, *Mori & Kallunki* 5790, 5989 (both NY). CHIRIQUÍ: Trail from Cerro Punta to headwaters of Río Caldera, 2250–2500 m, *Allen* 1434 (MO). Cloud forest at Monte Rey above Boquete, *Croat* 15774 (MO); *Croat & Porter* 15679 (MO). Cloud forest along continental divide on Cerro Colorado along upper mining road 20–28 mi from San Félix, 1200–1500 m, *Croat* 33317 (MO, NY). Bajo Chorro, 1840 m, *Davidson* 92 (A, F, US), 120 (A, F, US). Las Nubes, 1900–2200 m, *Luteyn* 3044 (CAS, DUKE, LL, MICH, MO, NY, PMA). Bajo Chorro, 2190–2210 m, *Luteyn* 3048 (DUKE, NY). Bajo Mono, NW of San Ramón, 1600–1700 m, *Luteyn* 3727 (DUKE, MO, NY). E slopes of Cerro Horqueta, 1700–1800 m, *Luteyn* 3753 (DUKE, NY), 3757 (DUKE, F, MO, NY). Las Nubes, 1900–2200 m, *Luteyn* 3811 (DUKE, NY). E slopes of Cerro Horqueta, 1700–1800 m, *Luteyn & Wilbur* 4605 (DUKE, MO). Cerro Colorado cloud forest along continental divide, 1200–1500 m, *Mori & Dressler* 7765, 7887 (both MO, NY). Palo Alto just E of Boquete, 1540 m, *Stern et al.* 1069 (GH, MO, US). E slopes of Cerro Horqueta, 1700–1800 m, *Wilbur & Luteyn* 19206 (DUKE). Trail along upper Río Chiriquí Viejo, 2 km N of Cerro Punta, *Wilbur et al.* 13087, 15373 (both DUKE, MO). Bajo Mono and Quebrada Chiquero, 1500 m, *Woodson & Schery* 574 (GH, NY), 576 (MO). Bajo Chorro, 1900 m, *Woodson & Schery* 632 (GH, MO, NY). COCLÉ: Trail to La Mesa N of El Valle, 1000 m, *Allen* 2721 (A, F, MICH, MO, NY, UC, US). N of El Valle, *Allen* 3637 (G, GH, MO, NY, S, US). La Mesa, 810 m, *Croat* 25330 (MO); *D'Arcy & D'Arcy* 6761 (MO). Between Cerro Pilón and El Valle de Antón, 700–900 m, *Duke & Dwyer* 13937, 13959 (both MO, UC). Cerro Pilón, 1000 m, *Dwyer & Lallathin* 8609A (NY). Trail to Los Llano beyond La Mesa, 800–860 m, *Luteyn* 3169 (DUKE). Trail beyond La Mesa to the E, *Luteyn & Kennedy* 1729 (DUKE, F, MO, NY, PMA). DARIÉN: Serranía de Pirre, 9–10 km N of Alto de Nique, 1520–1560 m, *Croat* 37869 (MO, NY). Serranía de Pirre, along headwaters of Río Escucho Ruido, ca. 16 km N of Alto de Nique, 1530–1550 m, *Croat* 37927 (MO, NY). Cerro Pirre, *Bristan* 604(2) (MO); *Duke* 6079 (MO). PANAMÁ: Cartí-El Llano-Tupile road, 15–16 km beyond Interamerican Highway, 400 m, *Busey* 365 (DUKE). Campo Tres, beyond Cerro Jefe, 500–800 m, *Croat* 27063 (MO). Cerro Jefe, *Duke* 8017(2) (MO). Cartí-El Llano-Tupile road, 15–16 km beyond Interamerican Highway, 400 m, *Kennedy et al.* 2409 (MO). 12 mi above Pan American Highway, along the Cartí-Tupile road, 200–500 m, *Liesner* 684 (MO). Campo Tres, beyond Cerro Jefe, 500–800 m, *Liesner* 549 (MO); Cartí-El Llano-Tupile road, 10–12 km N of Interamerican Highway, 500 m, *Luteyn & Wilbur* 4680 (DUKE, MO). El Llano-Cartí road, 12.7 km from Inter-American Highway, *Mori et al.* 4692 (NY). El Llano-Cartí road, 16–18 km above Inter-American Highway, *Nee & Tyson* 10956 (NY). El Llano-Cartí road, 8–12 km N of El Llano, *Nee et al.* 8745 (NY). Cerro Jefe, trail leading from summit W, *Witherspoon & Witherspoon* 8493 (MO, NY); Cerro Jefe, summit area, *Witherspoon et al.* 8281 (MO, NY). VERAGUAS: Road between Escuela Agrícola Alto Piedra and Calóvebora, 350–400 m, *Croat* 27394 (MO). Road beyond the Escuela Agrícola Alto Piedra, 800–1000 m, *Luteyn & Wilbur* 4573 (DUKE, MO, NY). 8.8 km from Escuela Agrícola Alto Piedra, NW of Santa Fé, *Mori & Kallunki* 3213 (NY). First branch of the Río Santa María, NW from Santa Fé, *Witherspoon & Dressler* 8920 (MO, NY).

6. **Cavendishia chiriquiensis** A. C. Smith, Ann. Missouri Bot. Gard. 28: 449. 1941. TYPE: Panama; Woodson & Schery 688 (NY, holotype; photo of holotype, DUKE, NY; MO, isotype).

Weakly erect, epiphytic *shrub* to 3 m tall, the stem base ca. 3 cm in diameter; mature branches terete, smooth to minutely striate, glabrous, tan, grayish red or reddish brown; immature branches and the twigs of the new growth terete to bluntly angled, smooth or striate, glabrous, tan, infrequently with caducous, globular glands on the recent growth. *Leaves* elliptic, 4.5–8 cm long, 1.5–3.5 cm wide, basally cuneate or sometimes attenuate, apically caudate acuminate, the acumen 1.5–2(–2.5) cm long, averaging $\frac{1}{4}$ – $\frac{1}{3}$ of the total leaf length, brownish to grayish green or tan when dry, glabrous or slightly puberulous at the base of the midrib when young, glabrescent; 3–5-plinerved, the midrib, the lateral nerves, and the veinlets impressed to slightly elevated and conspicuous above, all the veins raised beneath but usually only the midrib conspicuous, newly unfolding leaves often densely provided with caducous, globular glands on the upper surface and reddish glandular fimbriate beneath; petioles terete to subterete, sometimes flattened adaxially, rugose, 4–8 mm long, 1–1.5 mm in diameter, densely white puberulous when young becoming glabrate, tan to reddish brown. *Inflorescence* viscid, 6–9(–11)-flowered, the rachis complanate, bluntly angled, sometimes flexuous, smooth or minutely striate, glabrous, 1.5–4.5 cm long, ca. 1 mm in diameter at the base, pale green suffused with red when fresh but drying brick red, infrequently with a few scattered globular glands; floral bracts glabrous, slightly ribbed, smooth, rugose or muricate, oblong to oblanceolate, basally narrowed and truncate, apically acute or rounded, 15–25 mm long, 5–9 mm broad, red, each margin with 11–12, sessile, globular glands to 0.5 mm in diameter, these often caducous; pedicels terete to angled, swollen at both ends, minutely striate, glabrous, 4–7 mm long, 0.5–1 mm in diameter, pale green when fresh but drying brick red, provided with few scattered globular glands and cilia, especially distally; bracteoles linear to linear lanceolate, 1–2(–4) mm long, ca. 0.5 mm broad, with a hastate, callose thickened, apical gland which breaks off easily, a few globular glands at the margin. *Flowers* with the calyx glabrous, 3.5–4.5 mm long, pink at anthesis, the tube cylindric, smooth or rugose, 1.5–2(–2.5) mm long, 2–3.5 mm wide, basally slightly expanded, the expansion most noticeable in the early fruit, with numerous, scattered, globular glands not obscuring the surface of the tube, the limb campanulate to erect-spreading, rugose, ribbed, 1.5–2.5 mm long, with a few scattered glands similar to those of the tube, the lobes triangular, obtuse, 0.5–1 mm long, ca. 0.5 mm wide, erect after anthesis, completely or only marginally callose thickened but appearing almost completely callose thickened because of small size of the lobes, the lobes often breaking off with age, the sinuses broadly rounded or flat; corolla 16–24 mm long, 4–4.5 mm in diameter, reddish purple at the very base, purple above, the distal $\frac{1}{3}$ short pilose, the lobes triangular, obtuse, ca. 2 mm long; stamens 14.5–21 mm long, the filaments densely short pilose or glabrate, alternately 3 mm and 5–7.5 mm long, white, the anthers including tubules alternately 9.5–16.5 mm and 13–20 mm long, purplish orange, the thecae 3–6.5 mm long; style 17–23 mm long. *Berry* not seen.

Cavendishia chiriquiensis is endemic to western Panama and is most closely related to *C. panamensis*. Its distinctive characters are mentioned in the discussion of *C. panamensis*.

BOCAS DEL TORO-CHIRIQUÍ border: Chiriquí Trail, elfin forest at divide, *Kirkbride & Duke* 979 (MO, NY). CHIRIQUÍ: Boquete region, *Hagen & Hagen* 2033 (A, NY). Between Pinola and Divide, Chiriquicito-Caldera Trail, *Kirkbride & Duke* 849 (MO, NY). Slopes E of Cerro Horqueta, 1800–1900 m, *Luteyn & Wilbur* 4612 (BM, CAS, CR, DUKE, F, FSU, G, GH, K, LL, MICH, MO, MSU, NY, PMA, UC, US, WIS), 4617 (CAS, DUKE, F, GH, LL, MICH, MO, MSU, NY, UC, US). Cerro Colorado cloud forest on continental divide, 1200–1500 m, *Mori & Dressler* 7786 (MO, NY). Slopes E of Cerro Horqueta, 1700–1900 m, *Wilbur & Luteyn* 19323 (DUKE). Bajo Chorro, 1900 m, *Woodson & Schery* 688 (MO, NY).

7. ***Cavendishia complectens*** Hemsl., Biol. Centr. Amer., Bot. 2: 272. 1881.
TYPE: Costa Rica, *Endres* 257 (K, holotype; photo of holotype, DUKE, NY; W, isotype).

Epiphytic and terrestrial *shrubs*, 1–1.5 m tall, glabrous throughout; stem base to about 3 cm in diameter; mature branch erect or pendent, terete to bluntly angled; bark grayish to reddish brown. *Leaves* usually subsessile, amplexicaul, drying olive brown or dark green, oval to semiorbicular, (5–)8–16(–18) cm long, (4–)5.5–10(–13) cm wide, basally cordate with the basal lobes rounded, usually imbricate, apically obtuse to broadly rounded, rarely bluntly cuspidate; pinnately veined, the midrib impressed above, raised and conspicuous beneath, lateral nerves usually raised on both the surfaces, anastomosing to form a weak, collective marginal nerve, the veinlets slightly raised and obscure to conspicuous; petioles subterete, rugose, to 5 mm long. *Inflorescence* 1(–3) rachises per axil, the largest rachis rarely once branched at the base, 10–27(–60)-flowered, the rachis terete to bluntly angled, swollen at each floral node, 2–9(–20) cm long and 1–2 mm in diameter at anthesis, increasing to 3 mm diameter post-anthesis, pinkish green at anthesis, later turning purplish; floral bracts smooth or becoming ribbed after drying, elliptic to ovate lanceolate, rarely suborbicular, basally narrowed and somewhat auriculate, apically acute, (10–)11–16(–20) mm long, (5–)7–10(–17) mm wide, dark pink to red, marginally scarious and glandular fimbriate, ascending at anthesis but later spreading or perpendicular to the rachis; pedicels minutely striate or rugose, (2–)4–9(–11) mm long, 0.5–1 mm in diameter, pinkish green at anthesis but later turning purplish; bracteoles oblong to lanceolate, (1–)3–4(–7) mm long, (0.5–)1–2.5(–4) mm wide, basally slightly auriculate, apically rounded, marginally glandular fimbriate, dark pink. *Flowers* with the calyx (4.5–)6–8(–10) mm long, the tube hemispheric, basally not enlarged, smooth or minutely muricate, (1.5–)2–3.5(–6.5) mm long, 2.5–6 mm in diameter, purplish green, the limb campanulate, coriaceous, (2.5–)4–5(–5.5) mm long including the lobes, pale green, the lobes reniform, broadly ovate, rarely oblong, imbricate, (1.5–)2–3(–4) mm long, (1.5–)3(–4.5) mm broad, glandular fimbriate, whitish green, flaring at anthesis, later connivent and tightly curling around the base of the style; corolla cylindric or bottle-shaped, narrowed at the throat, (7–)8–10(–12) mm long, 4–6.5 mm in diameter at the widest part, white at the base, purplish black in the basal $\frac{1}{4}$, the mid-section green, the limb white, the lobes oblong, obtuse, 2–2.5 mm long, white;

stamens 7–8.5 mm long, the filaments white, alternately 2–3 mm and 3.5–4 mm long, with a few scattered distal hairs, the anthers orange including tubules alternately 4.5–6.5 mm and 5.5–7 mm long, the thecae 2–4 mm long; style 7–8.5 mm long, distally flaring. *Berry* 9 mm in diameter.

Cavendishia complectens is one of the easiest species to recognize because of its cordate, amplexicaul leaves. It has been collected a few times in eastern Darién Province, Panama, and in Chocó, Colombia, but is to be expected from western Panama also. It is common in the mountains of the Central Valley of Costa Rica and occurs rarely in Nicaragua.

DARIÉN: Cerro Pirre, *Bristan* 596; *Duke* 5321, 6103 (all MO). Serrania de Pirre, headwaters of Río Escucho Ruido, ca. 16 km N of Alto de Nique, 1530–1550 m, *Croat* 37936 (NY). W slope of Cerro Pirre, 1000 m, *Duke* 6595 (MO). Cerro Campamiento, *Duke* 15728(1) (MO). Cerro Pirre, 770–1380 m, *Duke* & *Elias* 12751 (F, MO, NY). Cuasi-Caná Trail on Cerro Campamiento, *Kirkbride* & *Duke* 1224 (MO, NY). Causi-Caná Trail between Cerro Campamiento and La Escalera, *Kirkbride* & *Duke* 1339 (MO, NY). N slopes of Cerro Pirre, 700–950 m, *Mori* & *Kallunki* 5465 (NY). Crest of Cuasi-Caná Trail, 1690 m, *Terry* & *Terry* 1577 (A, F, MO).

8. ***Cavendishia crassifolia*** (Benth.) Hemsl., Biol. Centr. Amer., Bot. 2: 273. 1881.

Thibaudia crassifolia Benth., Pl. Hartw. 65. 1840. TYPE: Mexico; Oaxaca, *Hartweg* 477 (K, holotype; photo of holotype DUKE, NY; FI, G, LD, LE, M, NY, US—fragments; W, isotypes).

T. mexicana Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 9(2): 530. 1842. TYPE: Mexico; Oaxaca, *Galeotti* 1813 (BR, holotype; photo of holotype DUKE, NY).

Proclesia veraguensis Klotzsch, Linnaea 24: 35. 1851. TYPE: Costa Rica; *Warszewicz* (B, holotype not seen, presumably destroyed photo of type, DUKE, NY).

Polyboea crassifolia (Benth.) Klotzsch, Linnaea 24: 31. 1851.

Cavendishia latifolia Hemsl., Biol. Centr. Amer., Bot. 2: 273. 1881. TYPE: Mexico; Chiapas, *Linden* 390 (K, holotype; photo of type DUKE, NY; F—fragments; G, isotypes).

C. veraguensis (Klotzsch) Hemsl., Biol. Centr. Amer., Bot. 2: 273. 1881.

Chupalon crassifolium (Benth.) Kuntze, Rev. Gen. Pl. 2: 383. 1891.

C. latifolium (Hemsl.) Kuntze, Rev. Gen. Pl. 2: 383. 1891.

Cavendishia guatemalensis Loesener, Bull. Herb. Boissier II. 3: 221. 1903. TYPE: Guatemala; Huehuetenango, *Seler* 3107 (B, holotype not seen, presumably destroyed; photo of type, DUKE, NY; GH, NY, US, isotypes).

C. smithii Hoerold, Bot. Jahrb. Syst. 42: 328. 1909. TYPE: Costa Rica, Cartago, Volcán Irazú, *Donnell Smith* 4876 (B, holotype not seen, presumably destroyed, photo of holotype DUKE NY; GH, US, isotypes).

C. costaricensis Hoerold, Bot. Jahrb. Syst. 42: 326. 1909. TYPE: Costa Rica; San José, La Palma, *Wercklé* 54 (B, holotype not seen, presumably destroyed, photo of type DUKE, NY, US; NY—fragments, isotype).

C. hoffmannii Hoerold, Bot. Jahrb. Syst. 42: 328. 1909. TYPE: Costa Rica; Cartago, Volcán Irazú, *Hoffmann* 141 (B, holotype not seen, presumably destroyed, photo and fragments of holotype, NY; photo of holotype DUKE).

C. chiapensis Brandege, Univ. Calif. Publ. Bot. 6: 188. 1915. TYPE: Mexico; Chiapas, *Purpus* 7342 (UC, holotype; photo of type DUKE, NY; F, GH, MO, NY, US, isotypes).

C. skutchii A. C. Smith, J. Wash. Acad. Sci. 27(7): 308. 1937. TYPE: Costa Rica; San José, El General, *Skutch* 2802 (US, holotype, photo of holotype, DUKE, NY; GH, MICH, NY—fragment, S, isotypes).

C. calycina A. C. Smith, Ann. Missouri Bot. Gard. 28: 447. 1941. TYPE: Panama; Chiriquí, Boquete, *Davidson* 157 (A, holotype; photo of holotype DUKE, NY).

C. guatemalensis var. *chiapensis* (Brandegee) L. O. Williams, Fieldiana Bot. 31: 169. 1965.

Epiphytic and terrestrial *shrubs*, 1–3 m tall, rarely arborescent and to 10 m tall with stem bases to 20 cm in diameter; mature branches terete or subterete,

smooth or striate, glabrous; bark brown to grayish brown; immature branches and twigs of the new growth subterete or bluntly angled, striate or ribbed, glabrous to densely pubescent, green or often red above and green beneath. *Leaves* oblong, elliptic, ovate or lanceolate, rarely oblanceolate or semiorbicular, 4–15(–22) cm long, 1.5–5(–11) cm wide, basally rounded, cuneate, subcordate, subtruncate or rarely short attenuate, apically acute to acuminate, often abruptly so and rarely rounded or cuspidate, green, olive green or brownish, sometimes metallic or slate blue when dry, glabrous or short pilose along the veins above and below; (3–)5–7(–9)-plinerved, innermost lateral nerves sometimes rising 1–2 cm above the base, midrib impressed above and raised beneath, always conspicuous, sometimes flattened adaxially, lateral nerves impressed or slightly raised distally above, raised beneath, the veinlets impressed or raised above, slightly raised but usually obscure beneath; petioles subterete, usually flattened adaxially, rugose, (3–)5–11(–17) mm long, 1–4 mm in diameter, glabrous, puberulent or pilose, reddish brown when dry. *Inflorescence* (4–)6–20(–40)-flowered, encircled at the base by bracts, the bracts glabrous to densely short pubescent, the pubescence often restricted to the margins or the apex, the rachis subterete to bluntly angled, (0.5–)1–5(–8) cm long, green or red, glabrous or pubescent with short white trichomes; floral bracts smooth or muricate, glabrous to densely short pilose, sometimes pubescent only along the margins or distally, oblong, ovate, elliptic to oblanceolate, basally narrowed and truncate, apically rounded or acute, (11–)17–26(–40) mm long, (5–)10–17(–27) mm wide, pink to dark red, sometimes provided with reddish, glandular fimbriae abaxially; pedicels often swollen distally, striate or ribbed, sometimes rugose, (3–)6–15(–20) mm long, 1–3 mm in diameter, pale green to dark rose red, glabrous or pilose, often with glandular fimbriae scattered along the length or densely aggregated distally; bracteoles oblong, ovate, lanceolate, linear lanceolate, rarely aristate, 1–4(–8) mm long, 0.5–2(–5) mm broad, glabrous to densely glandular fimbriate, sometimes ciliate. *Flowers* with the calyx glabrous to densely short pilose, (3.5–)4–6(–10.5) mm long, pale green to red, usually with few to many short, stout, glandular fimbriae, the tube cylindric, smooth or somewhat rugose, often somewhat pentagonal in cross section, 1.5–3(–4) mm long, not basally enlarged, the base often rounded or truncate and shallowly undulate, the limb cylindric to campanulate, usually somewhat spreading, (1.5–)2–3(–6) mm long including the lobes, the lobes triangular, rarely oblong, (0.5–)1–2(–5) mm long, connivent after anthesis, marginally glandular fimbriate, sinuses broadly rounded or acute; corolla cylindric to bottle-shaped, narrowed to the throat, (12–)15–20(–25) mm long, 4–5 mm in diameter, glabrous to short pilose, with or without scattered glandular fimbriae, pale pinkish to white at the base, the tube otherwise dark pink to red, the limb and the lobes white, the lobes deltoid, widely flaring at anthesis, 1–2 mm long; stamens 11.5–19 mm long, the filaments distinct or slightly coherent at the base, glabrous or distally pubescent, alternately 2–4 mm and 3.5–6.5 mm long, white or pinkish white, the anthers including the tubules alternately 7.5–14.5 mm and 10–16.5 mm long, yellow to orange, the thecae 2.5–6 mm long; style glabrous or rarely distally short pilose, (12–)14–19(–27) mm long. *Berries* 8–14 mm in diameter.

Cavendishia crassifolia is the most frequently encountered species of *Cavendishia* in southern Mexico and throughout montane Central America. It is recognized as a complex of wide-ranging, variable populations. Previous authorities have subdivided the complex into no fewer than 11 species. All of these species were described from single collections, from different geographical areas, and were based upon characters now seen to be unstable. The floral characters of the populations within this complex are virtually identical. Although there are local differences across the geographical range, there are no consistent morphological types associated with realistic geographical ranges, nor are there discontinuities in any combination of characters which could result in a meaningful subdivision. The complex also seems to range into South America where similar problems are to be expected.

Although specimens from the vicinity of Volcán Chiriquí were identified as *C. miconioides* by A. C. Smith, comparisons of the more numerous collections now available show these populations to be local variants of *C. crassifolia*.

BOCAS DEL TORO: Chiriquí Trail between Criollo and Quebrada Hondo, *Kirkbride & Duke* 793 (NY). Róbal Trail, N slopes of Cerro Horqueta, 1840–2160 m, *Allen* 4934 (G, MO, US). CHIRIQUÍ: Llanos area NE of El Hato del Volcán, *Allen* 1539 (MO); *Allen & Fairchild* 3463 (F, G, GH, MO, NY, S, US). S of Finca Lerida, 1840–2160 m, *Allen* 4771 (F, G, MO, US). Summit and SW face of Cerro Copete, 2770 m, *Allen* 4891 (F, G, GH, MO, US), 4893 (BM, BR, G, MO, US). Boquete, 1500 m, *Maurice* 718 (US). Llanos area NE of El Hato del Volcán, *Correa & Lazor* 1399 (DUKE). Slopes of Las Cumbres near Cerro Punta, *Croat* 13756 (MO); *Croat & Porter* 16068 (MO). Between Boquete and Monte Rey, *Croat* 15629 (MO). 2.2 km SW of Cerro Punta on road above IDAAN water tank, 2100–2250 m, *Croat* 26300 (MO, NY). Above San Félix along mining road, 17–18 mi off Panamerican Highway, 1200–1500 m, *Croat* 33096 (MO, NY). Above San Félix along mining road 18–27 mi off Panamerican Highway, 1200–1500 m, *Croat* 33113 (NY). E slope of Volcán Barú, 2400 m, *Davidse & D'Arcy* 10220 (NY). Llanos area NE of El Hato del Volcán, *Davidse & D'Arcy* 10369 (NY). W slope of El Barú, 2160–2460 m, *Davidse & D'Arcy* 10261 (NY). Bajo Chorro, 1840 m, *Davidson* 157 (MO), 343 (F). Volcán Chiriquí, Boquete District, 2770 m, *Davidson* 973 (DS, MO, US). Chiriquicito-Caldera Trail between Pinola and Divide, *Kirkbride & Duke* 842A (MO). Chiriquí Trail between Pinola and Quebrada Hondo, *Kirkbride & Duke* 911 (MO, NY). Chiriquí Trail between Quebrada Hondo and Divide, *Kirkbride & Duke* 924 (NY). Las Nubes, NW side of Cerro Punta, 2200–2300 m, *Luteyn* 3043 (DUKE, MO). Bajo Chorro, summit, 2200–2210 m, *Luteyn* 3046 (DUKE, F, MO, NY). Llanos area NE of El Hato del Volcán, *Luteyn* 3049 (CAS, DUKE, F, FSU, GH, LL, MICH, MO, MSU, NY, PMA, UC, US, WIS). Cerro Horqueta, 1800–1900 m, *Luteyn* 3079 (DUKE, MO). Bajo Mono Trail, NW of San Ramón, 1600–1700 m, *Luteyn* 3729 (DUKE, F, MO, NY); *Luteyn* 3741 (DUKE). Las Nubes vicinity, NW side of Cerro Punta, 2200–2300 m, *Luteyn* 3800 (DUKE). Bajo Chorro, 2360–2500 m, *Luteyn* 3835 (DUKE). Las Nubes vicinity, NW side of Cerro Punta, 2200–2300 m, *Luteyn & Wilbur* 4639 (DUKE, MO). Cerro Colorado, cloud forest along divide, 1200–1500 m, *Mori & Kallunki* 5883, 5894 (both NY); *Mori & Dressler* 7860 (MO, NY). Cerro Pando, on continental divide and Panama-Costa Rican border, ca. 16 km NW of El Hato, 2000–2482 m, *Mori & Bolten* 7289 (MO, NY). W side Volcán Barú, oak forest, 2000–2500 m, *Mori & Bolten* 7357 (MO, NY). Llanos area NE of El Hato del Volcán, *Seibert* 321 (MO). Finca Collins near Boquete, *Sullivan* 401 (FSU). Deep arid canyon, 5 mi NE of El Volcán, 1935–2000 m, *Tyson* 807 (FSU, MO). Dry windswept canyon, 8 mi NE of El Hato, 2500–2580 m, *Tyson* 830 (FSU), 840 (FSU, MO). Deep arid canyon, 5 mi NE El Volcán, 2160 m, *Tyson* 6343 (FSU, MO). W slope of El Barú, 1840–2160 m, *Tyson & Loftin* 5944 (DUKE, FSU, MO). W slope of El Barú, 2160–2460 m, *Tyson & Loftin* 5995 (DUKE, FSU, MO). W slope of El Barú, 2460–2770 m, *Tyson & Loftin* 6115 (DUKE, FSU). Valley of upper Río Chiriquí Viejo, 1300–1900 m, *White & White* 35 (MO, NY). Lava fields NE of El Hato near Aguacate, 1800–1900 m, *Wilbur et al.* 10969 (CAS, DUKE, F, GH, MICH, MO, NY); *Wilbur et al.* 10974 (DUKE, F, MO). Lava fields 4 mi NW of El Hato near Río Macho de Monte, 1800 m, *Wilbur & Teeri* 13076 (DUKE, F, MO). Las Nubes vicinity, NW of Cerro Punta, 2200–2300 m, *Wilbur & Teeri* 13206 (DUKE); *Wilbur & Teeri*

13222 (DUKE, F, GH, MO). Lava field and slopes beyond Volcán Chiriquí and Cerro Aguacate, 2000–2200 m, *Wilbur & Teeri* 13326 (BM, CAS, CR, DUKE, F, FSU, G, GH, K, LL, MICH, MO, MSU, NY, PMA, UC, US, WIS). Southern slopes of Cerro Horqueta, 2210 m, *Wilbur et al.* 13484 (DUKE, MO, NY), 17301 (DUKE). Llanos area NE of El Hato del Volcán, *Wilbur et al.* 15406 (BM, CAS, CR, DUKE, F, FSU, G, GH, K, LL, MICH, MO, MSU, NY, PMA, UC, US, WIS). Casita Alta to Cerro Copete, 2300–3300 m, *Woodson & Schery* 357 (GH, MO, NY). COCLÉ: Cerro Caracoral, elfin forests, *Duke & Dwyer* 15117(2) (NY); *Kirkbride* 1101 (MO, NY). VERAGUAS: Vicinity of Santa Fé, slopes of Cerro Tute, 925–1000 m, *Allen* 4340 (F, G, GH, MO, NY, US); *Mori* 6757 (NY). Trail up E side of Cerro Tute, to 1200 m, *Witherspoon & Dressler* 8845 (MO, NY).

9. ***Cavendishia darienensis*** Luteyn, *Brittonia* 28: 43. 1976. TYPE: Panama; Darién, Río Balsa, between Manene and Aretí, *Duke* 13509(6) (US, holotype, photo of holotype DUKE, NY; WIS, isotype).

Terrestrial and epiphytic *shrubs*, mature branches terete to subterete, slightly angled, minutely striate, glabrous, reddish to grayish brown when dry; immature branches and twigs of new growth subterete, ribbed, striate, densely short pilose or glabrous. *Leaves* oblong to oblong elliptic, 5.5–10 cm long, 2.5–4.5 cm wide, basally subcordate, apically obtuse, glabrous or with scattered, short trichomes along the base of the midrib and the lateral nerves, the margins of the young leaves often short pilose; 5-plinerved, the midrib and the lateral nerves strongly impressed proximally, plane to slightly elevated above distally, raised and conspicuous beneath and the leaves then bullate, the veinlets raised and conspicuous above, slightly raised but obscure beneath; petioles subterete, bluntly angled, rugose, 4–6 mm long, 1.5–2 mm in diameter, densely puberulent becoming glabrous. *Inflorescence* 26–28-flowered with the lowest few (up to 5) nodes sterile, encircled at the base by puberulent, ovate, apiculate bracts; rachis bluntly angled, striate, densely short pilose, 8.5–9.5 cm long, 2–2.5 mm in diameter; floral bracts prominently striate on both the surfaces with conspicuous midrib, lanceolate, (14.5–)18.5–23 mm long, 6–9 mm wide, basally cuneate and strongly concave, apically long acuminate, marginally glandular fimbriate, densely short hirsute on both the surfaces with white trichomes 0.2–0.4 mm long, pink (according to label data); pedicels subterete, 1–2.5 mm long, 0.5–1 mm in diameter, short white pilose; bracteoles lanceolate, apically long acuminate, striate, (8–)13–16 mm long, 3.5–4.5(–6.5) mm broad, marginally glandular fimbriate, densely short pilose as the floral bract, clasping the base of the calyx, slightly spreading distally. *Flowers* with the calyx 7–9.5 mm long, abruptly widened at the junction of the tube and the limb, short pilose from the base of the tube to the tip of the lobes, the tube smooth, subglobose, slightly rugose, basally rounded, 2–2.5 mm long, the limb cylindric to slightly spreading, conspicuously striate as the lobes, 5.5–7 mm long including the lobes, the lobes long triangular, 2–4 mm long, 2–2.5 mm wide, erect after anthesis, marginally scarious and eglandular, pubescent within; sinuses obtuse; corolla bluntly 5-angled opposite the calyx sinus, densely short pilose without, glabrous within and at the base where surrounded by calyx limb, 11.5 mm long, 3–3.5 mm in diameter, with scattered, short, red, clavate fimbriae on the surface, the lobes obtuse, erect; stamens alternately 8–8.5 mm and 8.5–9 mm long, the filaments weakly short pubescent distally, alternately 2–2.5 mm and 3.5–4 mm long, the

anthers alternately either 6–6.2 mm or 6.5–7 mm long, the thecae 2–2.5 mm long; style 9.5–10.5 mm long. *Berry* not seen.

Cavendishia darienensis is found in Darién, Panama and adjacent Chocó, Colombia at 100–950 m elevation. It is most closely allied to *C. allenii*, another lowland species but endemic to central Panama. The two species share similar gland types on the calyx lobes and bracteoles, and in addition, both possess prominently nerved or striate floral bracts, bracteoles and calyces.

DARIÉN: Between upper Río Membrillo and Camp 7 on the construction road to San Blas, *Duke 10888(2)* (MO). Río Balsa, between Manene and Aretí, *Duke 13509* (MO, US, WIS). Cerro Pirre, *Mori & Kallunki 5483* (MO, NY).

10. *Cavendishia fusiformis* Luteyn, *Brittonia* 28: 42. 1976. TYPE: Panama, *Kirkbride & Duke 1276* (MO, holotype; photo of holotype, DUKE, NY; NY, isotype).

Epiphytic *shrub*; immature branches and twigs of the new growth terete, somewhat rugose, moderately hirsute or glabrate, trichomes 1–2 mm long, tan to tawny yellow. *Leaves* elliptic or oblong elliptic, (4.5–)9–14 cm long, (1–)2–4 (–6) cm wide, basally narrowing and obtuse, apically acuminate, grayish or brownish green above and tan beneath when dry, sparsely short pilose along the nerves above, moderately pilose or glabrate beneath with tawny yellow trichomes; 3(–5)-plinerved, the midrib weakly impressed or plane above, raised and prominent beneath, the lateral nerves weakly impressed or more commonly elevated on both the surfaces as the veinlets; petioles terete or infrequently flattened adaxially, rugose, 4–7 mm long, 2 mm in diameter, hirsute. *Inflorescence* obconic or fusiform at anthesis, ca. 20-flowered, the lowest nodes sterile, circumscribed at the base by striate bracts; rachis glabrous, smooth, fusiform, 3–8 cm long, 5–6 mm in diameter medially, the nodes congested; floral bracts glabrous, striate, marginally scarious, oblong obovate, basally narrowing and rounded, apically rounded and emarginate, commonly tearing, 25–35 mm long, 13–18 mm wide, red to rose pink, with subsessile, capitate, red glands located at the base; pedicels subterete, glabrous, ca. 1 mm long, 1–1.5 mm in diameter; bracteoles oblong or oblanceolate, imbricate, basally clasping the calyx, apically rounded and shallowly emarginate, 25–30 mm long, ca. 10 mm broad, with subsessile, capitate, red glands as on the floral bracts. *Flowers* with the calyx glabrous, 11–15 mm long, the tube barrel-shaped, smooth, 2.5–4 mm long, not enlarged basally, the limb erect, spreading, submembranaceous, striate, 9–12 mm long including lobes, the lobes linear oblong, acute, 3–6 mm long, erect after anthesis, the few, stout, glandular marginal fimbriae occasionally distally fused, sinuses obtuse to broadly rounded; corolla glabrous, membranaceous basally and subcoriaceous apically, 34–35 mm long, 6–7 mm in diameter, white with green tips; stamens alternately 10–11.5 mm and 12–13.5 mm long, about $\frac{1}{3}$ the length of the corolla, the filaments distinct or slightly coherent basally, glabrous, alternately 1–2 mm and 3.5–4.5 mm long, the long filaments conspicuously narrowed and thin distally, the anthers including the tubules alternately 8–9 mm and 9–10.5 mm long, the thecae smooth, 2.5–3 mm long, the tubules dehiscing by

short, oblique pores or oval clefts 1–1.5 mm long; style 33–37 mm long. *Berry* not seen.

Cavendishia fusiformis is endemic to eastern Darién Province. It is closely related to a group of Colombian species described by A. C. Smith; *C. glandulosa*, *C. venosa*, *C. speciosa*, *C. micayensis*, and *C. chlamydantha*. As a group these species are unique in having stamens which are usually one-third to one-half the length of the corolla, rachises which are distinctly clavate or fusiform in shape, calyx limbs tending to be elongate and infundibuliform, and corollas which are membranaceous below and somewhat coriaceous above.

DARIÉN: Cerro Pirre, *Bristan* 542(2) (MO); *Duke* 6119 (MO), *Gentry & Clewell* 6952 (MO). Caña-Cuasí Trail between Cerro Campamiento and La Escalera to "páramo," E of Tres Bocas, *Kirkbride & Duke* 1276 (DUKE, MO, NY). Cerro de Garagára, Sambú basin, 500–974 m, *Pittier* 5651 (US). Cana-Cuasí Trail, 1690 m, *Terry & Terry* 1567 (A, F, MO).

11. ***Cavendishia gentryi*** Luteyn, *Brittonia* 28: 400. 1976. TYPE: Panama; Darién, Cerro Tacarcuna, *Gentry & Mori* 13971 (MO, holotype; photo of holotype, NY; DUKE, NY, isotypes).

Epiphytic *shrub*, mature branches terete, smooth, glabrate, brown; immature branches and twigs of the new growth terete, smooth, reddish brown, densely pilose with white hairs to 4 mm long. *Leaves* elliptic to ovate elliptic, 8–13 cm long, 3.5–5.5 cm wide, basally rounded, apically abruptly acuminate, brownish green when dry, densely pilose beneath with hairs to 2 mm long, scattered pilose above; 3(–5)-plinerved, the midrib, the lateral nerves and the primary veins impressed and conspicuous above, elevated beneath, the veinlets slightly elevated above, obscure beneath; petioles terete, rugose, 5 mm long, 2 mm diameter, densely pilose with tan hairs to 3 mm long. *Inflorescence* short racemose, 6-flowered; rachis terete, striate, densely pilose, ca. 2.5 cm long; floral bracts lanceolate, long acuminate, 16–23 mm long, 4–6 mm wide, densely pilose marginally, scattered pilose on the lamina, trichomes to 2 mm long; pedicels swollen distally, striate, densely pilose, 8–12 mm long; bracteoles not seen. *Flowers* with the calyx densely pilose, 13–13.5 mm long, pink, the tube spherical, 3.5–4.5 mm long and broad, not expanded, the limb short cylindric or somewhat spreading, 9–9.5 mm long including the lobes, the lobes linear lanceolate, acute, 8 mm long, ca. 2 mm broad at the base, erect after anthesis, marginally with 3–4 gland-tipped fimbriae on each side, sinuses acute; corolla (past anthesis) cylindric, ca. 20 mm long, scattered pilose with the hairs denser at the lobe tips; stamens ca. 16 mm long, the filaments alternately ca. 1 mm and 3 mm long, the anthers including tubules alternately ca. 15 mm and 13 mm long, the thecae 3–4 mm long; style ca. 21 mm long. *Berry* not seen.

Cavendishia gentryi, endemic to Darién Province, is most closely related to *C. darienensis*. The two species are easily separated however, by the leaf shape and by the shorter rachis with fewer flowers, the nonstriate floral bracts, longer pedicels, more densely pilose calyx, and glandular calyx lobes of *C. gentryi*.

DARIÉN: Cerro Tacarcuna, elfin forest at top of W peak, 1800–1850 m, *Gentry & Mori* 13971 (DUKE, MO, NY).

12. **Cavendishia laurifolia** (Klotzsch) Benth. & Hook., Gen. Pl. 2: 570. 1876.

Polyboea laurifolia Klotzsch, Linnaea 24: 31. 1851. TYPE: Guatemala; Alta Verapaz, Warshawicz (B, lectotype, not seen, presumably destroyed; photo of lectotype, DUKE, F, NY).

Chupalon laurifolium (Kl.) Kuntze, Rev. Gen. Pl. 2: 383. 1891.

Cavendishia tuerckheimii Hoerold, Bot. Jahrb. Syst. 42: 323. 1909. TYPE: Guatemala; Alta Verapaz, Cobán, Tuerckheim 64 (B, holotype, not seen, presumably destroyed, photo of type DUKE, NY; GH, NY, US, isotypes).

Epiphytic or terrestrial *shrubs*, 1–3 m tall; stem base 2.5–5 cm in diameter; mature branches arching, terete, striate, glabrous; bark tan to grayish brown; immature branches and twigs of the new growth subterete or flattened with blunt angles, striate, reddish brown, densely puberulous and often with short, reddish, glandular fimbriae. *Leaves* slightly bullate when fresh, drying bullate or flat, lanceolate, ovate or lance elliptic, (3.5–)6–12.5 cm long, (1–)2–4 cm wide, basally rounded or obtuse, rarely subcordate, apically acuminate, tan or olive brown when dry, puberulous above along the proximal portions of the midrib and the lateral nerves, glabrous beneath; 3–5-plinerved, the midrib and the lateral nerves impressed above, the veinlets raised and conspicuous above, the midrib and the lateral nerves raised and conspicuous beneath, veinlets plane or raised but obscure beneath; petioles subterete, smooth, striate, or commonly rugose, 2–5 mm long, 0.5–1.5 mm in diameter, densely puberulous adaxially, reddish brown. *Inflorescence* (8–)17–32(–45)-flowered with the lowermost nodes bracteolate but sterile; rachis subterete, striate, weakly muricate, glabrous, 4–15(–20) cm long, 1.2 mm in diameter, rose pink at anthesis but turning whitish or pale green; floral bracts muricate, glabrous, oblong, obovate, or oblanceolate, 7–13 mm long, 3.5–6.5(–10) mm wide, basally narrowed, apically obtuse to broadly rounded, rarely acute, marginally scarious and glandular fimbriate, the bract concave, oriented perpendicular to or somewhat recurved with respect to the rachis, deep rose pink; pedicels swollen distally, striate, 10–17 mm long at anthesis, 0.5–1 mm in diameter, 10–22(–26) mm long in fruit, rose pink at anthesis but turning whitish or pale green, provided with reddish, glandular fimbriae 0.3 mm long when young, these caducous; bracteoles oblong to ovate, 1–2.5 mm long, 0.5–1(–2) mm broad, basally slightly auriculate, marginally glandular fimbriate, rose pink. *Flowers* with the calyx 2.5–3.5 mm long, green in bud, dark wine red at anthesis, later turning green, the tube cylindric but slightly pentagonal in cross section, rugose, 0.5–1 mm long, 2.5–3(–4) mm in diameter, basally slightly expanded, densely covered in bud by reddish, glandular fimbriae, the limb broadly campanulate, muricate, 1.5–3 mm long including the lobes, densely glandular fimbriate, these fimbriae usually persisting to fruit, the lobes triangular or oblong, (0.2–)0.5–1 mm long, connivent after anthesis, marginally thin and glandular fimbriate, sinuses acute in bud, becoming broadly rounded to flat at anthesis; corolla bottle-shaped, bluntly 5-angled opposite calyx lobes, constricted basally, (6.5–)8–10(–12) mm long, 5.5–6.5 mm in diameter at the widest point, the tube with scattered glandular fimbriae, white for lowest $\frac{2}{3}$, dark rose red in the upper $\frac{1}{3}$ plus the limb and the lobes, the lobes oblong, acute, slightly flaring at anthesis; stamens alternately either 6–7 mm or 7–8.5 mm long, the filaments densely puberulous in distal

half, alternately either 1.5–3 mm or 2.5–4 mm long, white to pinkish white, the anthers including tubules alternately 4–5.5 mm and 5.5–7 mm long, orangish brown to maroon, the thecae 1.5–3 mm long; style 8–9 mm long. *Berry* glabrous, 6–7 mm in diameter.

The three collections cited below are the first modern records of *C. laurifolia* outside its principal range of the Mexico-Guatemalan border area. Although there existed a Warszewicz collection (BR, W) which bore the label data "Costa Rica et Veragua," Luteyn (1976) doubted the credibility of this data because of other questionable Warszewicz collection sites. The recent collections from Darién however verify the presence of *C. laurifolia* in Panama.

DARIÉN: Summit of Cerro Pirre, cloud forest, 1000–1400 m, *Gentry & Clewell* 7107 (DUKE, MO). Serrania del Darién, W of Unguia on Panama-Colombia border, 1150 m, *Gentry et al.* 17036 (NY). W slope of Cerro Pirre, 1000 m, *Duke* 6585 (MO).

13. ***Cavendishia megabracteata*** Luteyn, *Brittonia* 28: 49. 1976. TYPE: Panama; *Luteyn & Wilbur* 4594 (DUKE, holotype; F, GH, LL, MICH, MO, NY, PMA, US, isotypes).

Terrestrial or epiphytic *shrubs* to 2.5 m tall, stem base to 5 cm in diameter; mature branches terete, minutely striate, glabrous; bark brown, drying grayish to reddish brown; immature branches and twigs of the new growth terete to bluntly angled, striate, glabrous, reddish brown when dry. *Leaves* ovate, lanceolate, lance elliptic or oblong, (4–)8–12(–15) cm long, (1–)2.5–7 cm wide, basally obtuse, rounded to truncate, apically acuminate, often abruptly so, dark olive to grayish brown when dry, usually puberulous at the base of the midrib and the lateral nerves on the upper surface; 5–7-plinerved, the midrib and the inner lateral nerves moderately or weakly impressed above but sometimes plane or raised distally, the outer lateral nerves and the veinlets raised and usually conspicuous above, rarely impressed, all the nerves raised beneath but the veinlets often obscure; petioles subterete, often flattened adaxially, rugose, rarely striate, 4–10(–13) mm long, 1–2.5(–3) mm in diameter, glabrous to densely puberulent adaxially when young, often glabrate and reddish brown at maturity. *Inflorescence* (2–)5–9(–12)-flowered, often lowest one or two nodes sterile, obconic to spherical in bud; rachis coarsely and bluntly angled, striate, glabrous, (0.6–)0.8(–3.5) cm long, ca. 2 mm in diameter, cream colored and often suffused with pink when fresh, rarely with a few clavate glands or cartilaginous teeth at the base; floral bracts often translucent when dry, glabrous, smooth with minute, red, clavate, glandular fimbriae abaxially, oblong, obovate or rarely subrotund, basally narrowed and somewhat clasping, apically rounded, usually deeply emarginate (2–)3–6(–7) cm long, (1–)1.5–2.5(–4.5) cm wide, pale purplish to bright rose or dark pink when fresh; pedicels swollen distally, striate, glabrous, (8–)10–16(–19) mm long, (0.5–)1(–1.5) mm in diameter, cream colored and often suffused with pink when fresh, rarely weakly glandular at the distal end; bracteoles with or without prominent midrib, ovate, lanceolate, lance elliptic or nearly linear, 1.5–2(–5) mm long, 0.5–1.5(–4) mm wide, apically callose thickened; calyx glabrous, 7–11(–13) mm long, cream colored and often suffused with

pink, the tube cylindric, ribbed, 2–5 mm long, 3–5 mm in diameter at the base, basally enlarged and deeply lobed, the lobes straight to flaring outward and extending well below articulation, the limb cylindric to slightly spreading, smooth or minutely papillate, (4–)5–7.5(–9) mm long including the lobes, the lobes triangular, (1–)1.5–2(–2.5) mm long, erect after anthesis, the tips completely glandular callose thickened or callose thickened apically, centrally or only marginally, sinuses subacute when fresh, but drying obtuse to broadly rounded, rarely flat; corolla slightly constricted basally and at the throat, often translucent when dry, 31–40(–43) mm long, 7–9 mm in diameter, glabrous or rarely pilose distally, the tube dull or glossy white, often basally pink to pinkish below, grading through violet to pale purple above, the limb white, the lobes oblong, obtuse, 1.5–2 mm long, reflexed at anthesis, white but sometimes marginally purple; stamens 24.5–36 mm long, the filaments densely puberulous distally, alternately 2.5–7.5 mm and 7.5–13.5 mm long, white, the anthers including tubules alternately 16–26.5 mm and 21.5–32.5 mm long, yellowish to tawny orange, the thecae 6–13 mm long; style 32–41 mm long. *Berry* not seen.

Cavendishia megabracteata, endemic to western Panama, may be distinguished by the combination of large and usually emarginate floral bracts, short rachis, and few-flowered inflorescences which are obconic or spherical in bud. Both the floral bracts and the corolla are extremely thin and translucent when dry. The size, shape and texture of the floral bracts alone serve to distinguish this species from all other Mexican-Central American species of the genus.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 1840–2160 m, *Allen* 4974 (G, MO, US). CHIRIQUÍ: Bajo Chorro, 1900–2500 m, *Allen* 1427 (MO, US). Bajo Mono-Róbalo Trail, 1540–2160 m, *Allen* 4841 (G, MO, US). Cerro Horqueta, 1700–2100 m, *Cochrane et al.* 6258 (WIS). Bajo Chorro, 1900–2500 m, *Davidson* 86 (F, MO). Cerro Horqueta, 1700–2100 m, *Dwyer et al.* 453 (MO); *Hagen & Hagen* 2034 (NY), 2047 (GH, NY), 2175 (GH, NY); *Lewis et al.* 439 (DUKE, MO, SCZ); *Luteyn* 3078 (DUKE, MO, NY), 3758 (CAS, DUKE, F, GH, MICH, MO, NY, US), 3789 (DUKE). Slopes E of Cerro Horqueta, 1700–2000 m, *Luteyn & Wilbur* 4594 (DUKE, F, GH, LL, MICH, MO, NY, PMA, UC, US). Between Alto de Las Palmas and Cerro Horqueta, 2100–2268 m, *Maxon* 5446 (US); *Pittier* 3206 (F, NY, US). Cerro Hornitos, 40 km NW of Gualaca, cloud forest at 2233 m, *Mori & Boulton* 7497 (MO, NY). Cerro Horqueta, Finca Collins, *Sullivan* 409 (FSU). Slopes E of Cerro Horqueta, 1700–2000 m, *Wilbur & Luteyn* 19227 (DUKE, MO, NY). Cerro Horqueta, 1700–2100 m, *Wilbur et al.* 13458 (DUKE, F, GH, LL, MICH, MO, NY, PMA, US). Bajo Mono, 1840 m, *Wilbur et al.* 13530 (DUKE, F, GH, MO, NY, US). Bajo Chorro, 1900–2500 m, *Woodson & Schery* 619 (GH, MO, NY), 692 (MO).

14. *Cavendishia melastomoides* (Klotzsch) Hemsl., Biol. Centr. Am., Bot. 2: 273. 1881.

Socratesia melastomoides Klotzsch, Linnaea 24: 23. 1851. TYPE: Costa Rica, *Warszewicz* (B, holotype, not seen; photo DUKE, NY).

14a. *Cavendishia melastomoides* var. *coloradensis* Luteyn, Brittonia 28: 401. 1976. TYPE: Panama, *Mori & Dressler* 7776 (NY, holotype; MO, isotype).

Epiphytic *shrub*, mature branches pendent, terete, smooth, glabrous, tan to reddish brown when dry; immature branches subterete, bluntly angled, striate, glabrous or rarely sparsely short pilose, provided with tiny, reddish,

caducous glands. *Leaves* elliptic, lanceolate, or ovate lanceolate, (3–)6–10 cm long, (2–)2.5–3.5 cm wide, basally rounded or cuneate, apically long acuminate or caudate acuminate, brownish green to tan when dry, glabrous; 3(5–)-plinerved, the midrib impressed and prominent above or somewhat plane distally, raised and conspicuous beneath, the lateral nerves slightly raised on both the surfaces or rarely impressed above, conspicuous only above; petiole subterete, flattened adaxially, rugose, (3–)4.5–9 mm long, 0.5–1.5 mm in diameter, glabrous or densely short pilose, becoming glabrate, reddish brown. *Inflorescence* usually with all parts viscid, 6–10-flowered; rachis subterete or bluntly angled, glabrous, (2–)2.5–3.5(–4.5) cm long, and 1–1.5 mm in diameter with scattered red, clavate glands; floral bracts glabrous, oblong, apically rounded, basally slightly clasping, 6–10 mm long, 3–6 mm wide; pedicels striate, ribbed, glabrous, 10–19 mm long, 0.5–1 mm in diameter, with glands as on the rachis; bracteoles strongly nerved, somewhat striate, broadly ovate to semiorbicular, apically rounded and apiculate, the apiculum callose thickened, basally auriculate, 2.5–4.5 mm long and broad. *Flowers* with the calyx glabrous, (3–)4.5–7.5 mm long, red, the tube smooth or rugose, 5-angled, 1–2(–3) mm long, broadly enlarged basally with the enlargement perpendicular to the calyx axis, the limb cylindric or somewhat spreading, smooth or rugose, (2–)2.5–4(–6.5) mm long including the lobes, the lobes triangular, (0.5–)1–1.5 mm long, erect after anthesis, completely callose thickened and glandular, sinuses obtuse or broadly rounded and almost flat; corolla slightly narrowed at the throat, the distal portion often curving upwards, 29–32 mm long, 3–7 mm in diameter, glabrous, blue (fide *Mori & Dressler 7776*); stamens ca. 26.5 mm long, the filaments glabrous, alternately 3.5 mm and 8 mm long, the anthers including tubules alternately 25 and 20 mm long, the thecae 6–7.5 mm long; style ca. 31 mm long. *Berry* not seen.

Cavendishia melastomoides var. *coloradensis* is endemic to Cerro Colorado, Chiriquí Province. It differs from the other two varieties of *C. melastomoides* (var. *melastomoides* and var. *albiflora* both from Costa Rica) primarily in its broadly ovate to semiorbicular bracteoles which have callose-thickened, apiculate tips.

CHIRIQUÍ: Cerro Colorado copper mine development, 28 mi above San Félix, 1200–1500 m, *Croat 33211* (MO, NY). Cloud forest along continental divide on Cerro Colorado, on upper mining road 20–28 mi from San Félix, 1200–1500 m, *Croat 33351* (MO, NY). N of San Félix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mining road, *Mori & Kallunki 5987* (MO). Cerro Colorado, 50 km N of San Félix on the continental divide, 1200–1500 m, *Mori & Dressler 7776* (MO, NY).

15. ***Cavendishia morii*** Luteyn, *Brittonia* 28: 401. 1976. TYPE: Panama, *Bristan 587* (DUKE, holotype; photo NY; MO, isotype).

Epiphytic *shrub*, mature branches and twigs of the new growth terete, striate, glabrous, tan to reddish brown when dry, sometimes glaucous. *Leaves* oblong, elliptic, ovate elliptic, (7–)10–14(–16) cm long, (3–)4–6 cm wide, basally rounded, obtuse or subtruncate, apically long acuminate or abruptly short acuminate, brown or olive brown when dry, glabrous; 5(7)-plinerved, midrib and lateral nerves slightly impressed above, raised and prominent beneath, the

veinlets slightly raised but obscure on both the surfaces; petioles terete, striate, (4-)7-10(-14) mm long, 2-2.5 mm diameter, sparsely pilose when young, glabrous at maturity, dark reddish brown. *Inflorescence* 15-25-flowered; rachis bluntly angled, smooth or slightly striate, glabrous, (2.5-)7-9 cm long, 2-4 diameter at base; floral bracts smooth, glabrous, elliptic, 15-20 mm long, 8-10 mm broad, basally obtuse, apically rounded to obtuse, reddish; pedicels swollen distally, striate, glabrous, 8-10 mm long, 1 mm diameter at anthesis, later lengthening to 17 mm long; bracteoles ovate lanceolate, ca. 1.5 mm long, 0.7 mm broad, apically acute, glandular callose thickened marginally and for the distal $\frac{1}{2}$. *Flowers* with the calyx glabrous, ca. 5 mm long, the tube short cylindric, coarsely ribbed, ca. 1.5 mm long, strongly enlarged basally, the limb erect and spreading to slightly campanulate, rugose, ca. 3.5 mm long including the lobes, the lobes broadly triangular to somewhat ovate apiculate, 1 mm long, erect after anthesis, completely glandular callose thickened, the sinuses obtuse; corolla slightly narrowed at the base and the throat, 18-20 mm long and ca. 4.5 mm in diameter, glabrous, the lobes triangular or oblong, obtuse, ca. 1 mm long, the tips callose thickened; stamens 18.5-19 mm long, the filaments pilose in the distal $\frac{1}{2}$, alternately ca. 2 mm and 4 mm long, the anthers including tubules alternately ca. 18 mm and 16 mm long, the thecae 5.5-6.5 mm long; style ca. 19 mm long. *Berry* spherical, glabrous, ca. 11-12 mm diameter.

Cavendishia morii, endemic to Darién, is most closely related to *C. subfasciculata*. Together they share similar calyx and bracteole gland types and the unique character of callose-thickened corolla lobes. *Cavendishia morii* may be distinguished from *C. subfasciculata* by its longer, more floriferous rachises, its inflorescences fusiform in bud, its apically nonemarginate floral bracts, and smaller flowers.

DARIÉN: Cerro Pirre, *Bristan* 587(3) (DUKE, MO); *Duke & Elias* 13810 (DUKE, MO). Summit of Cerro Pirre, 1000-1400 m, *Gentry & Clewell* 7077 (DUKE, MO); *Gentry & Clewell* 7091 (MO). Cloud forest, Cuasí-Cañá Trail between Cerro Campamiento and La Escalera, E of Tres Bocas, *Kirkbride* 1306 (MO). Lower montane cloud forest, N slopes of Cerro Pirre, 700-950 m, *Mori & Kallunki* 5467 (MO, NY).

16. ***Cavendishia panamensis*** Luteyn, *Brittonia* 28: 47. 1976. TYPE: Panama; Chiriquí, Boquete District, *Luteyn* 3056 (DUKE, holotype; F, GH, LL, MICH, MO, NY, PMA, US, isotypes).

Erect, often arching, terrestrial *shrub*, 2.5-3 m tall; stem base ca. 2.5 cm in diameter; mature branches terete, glabrous, ca. 1 cm in diameter; bark yellowish brown; immature branches and twigs of the new growth bluntly angled or ribbed, minutely striate, glabrous. *Leaves* elliptic, lance elliptic to ovate lanceolate, 9-16 cm long, 3-6 cm wide, basally acute to narrowly obtuse, rarely rounded, apically acuminate to somewhat caudate acuminate, olive green to grayish green above and tannish green beneath when dry, glabrous but with scattered, elevated, reddish globular glands, the glands 0.1-0.2 mm in diameter along the upper leaf surface, often caducous usually leaving a reddish or blackish papillate scar; 5(-7)-plinerved, the innermost lateral nerves often arising 2-3 cm above the

base, the midrib impressed above, raised and conspicuous beneath, the lateral nerves impressed above becoming plane to slightly elevated distally with the outer lateral nerves often obscure beyond the middle, raised and conspicuous beneath, the veinlets raised and usually conspicuous above, obscure to slightly raised beneath; petioles terete, slightly flattened adaxially, rugose, (2.5–)6–8 (–10) mm long, 2–2.5 (–3.5) mm in diameter, glabrous or infrequently puberulent, golden tan. *Inflorescence* viscid, 11–21 (–37)-flowered, often the several lowest nodes sterile; rachis flattened, gradually tapering and often flexuous distally, conspicuously ribbed and minutely striate, glabrous or rarely puberulent, (3–)8–17 cm long, to 5 mm in diameter at the base, pink to dark pink when fresh with minute, peltate, globular reddish glands along its length and especially at the base; floral bracts glabrous or sparsely ciliate along the distal $\frac{1}{3}$ of the margin, oblong to oblanceolate, rarely obovate, basally narrowed to a slightly clasping base, apically rounded or narrowly obtuse to acute, (2–)3–5 cm long, (0.6–)1–2 cm wide, pink, marginally with 7–23 dark red, globular, peltate or sessile glands ca. 0.7 mm in diameter; pedicels subterete, swollen distally, striate, glabrous (11–)15–19 mm long, 1–1.5 mm in diameter, pink, with few, scattered, globular, reddish glands; bracteoles ovate to lanceolate, 1.5–2 (–4) mm long, 1–2 mm wide, pink, with few, scattered, dark red, globular glands marginally and apically. *Flowers* with the calyx glabrous, 4–6 mm long, the tube cylindric or spreading, rugose to strongly ribbed, 1.5–2 mm long, 2.5 mm in diameter, not basally enlarged, green, usually with dark red, globular to disc-shaped, peltate glands obscuring the surface, the limb cylindric campanulate, smooth (2.5–)3–3.5 mm long including lobes, pale green to pinkish with scattered, globular to disc-shaped, peltate glands, the lobes triangular, obtuse, 1–1.5 mm long, 1.5 mm broad, erect after anthesis, marginally glandular callose thickened with the glands contiguous at the lobe apices, pinkish green with dark pink margins; sinuses broadly rounded; corolla constricted basally, narrowed to the throat, 2.5–3.5 cm long, 8–10 mm in diameter, glabrous, or pilose and glabrous at the constricted base, white, the lobes triangular, obtuse, 1–2 mm long; stamens 27–30 mm long, the filaments slightly coherent basally, strigose distally, alternately 4–6 mm and 10–13.5 mm long, white, the anthers including the tubules alternately 17–20.5 mm and 25–27 mm long, yellow, the thecae 7.5–11 mm long; style 25–31 mm long. *Berry* not seen.

Cavendishia panamensis like *C. chiriquiensis* is endemic to western Panama. Both species are characterized by glandular-margined floral bracts and bracteoles, and gland-covered calyx tubes. In these respects they are reminiscent of *C. pseudostenophylla*. However, the linear leaves of *C. pseudostenophylla* at once distinguish that species. *Cavendishia panamensis* differs from *C. chiriquiensis* by a basic difference in calyx lobe glands. In *C. panamensis* the callose-thickened portion of the calyx lobe is strictly marginal, while in *C. chiriquiensis* the entire calyx lobe is callose thickened and appears occasionally to break off.

CHIRIQUÍ: Boquete District, Bajo Chorro Trail, *Davidson* 86 (US); *Luteyn* 3056 (DUKE, F, GH, LL, MICH, MO, NY, PMA, US). Cerro Horqueta, 1800–1900 m, *Luteyn* 3080 (DUKE). VERAGUAS: Cerro Tute, NW of Santa Fé, *Mendietz* 562 (PMA).

17. **Cavendishia pseudostenophylla** Luteyn, Brittonia 28: 46. 1976. TYPE: Panama; Bocas del Toro, Chiriquí Trail, *Kirkbride & Duke 779* (NY, holotype, photo of type DUKE, NY; MO, isotype).

Epiphytic *liana*, mature branches terete, minutely striate, puberulent brown when dry; bark reddish brown; immature branches and twigs of the new growth subterete to bluntly angled, minutely striate, puberulent, brown. *Leaves* linear lanceolate to linear elliptic, 9–14 cm long, 1–1.5 cm wide, basally broadly obtuse or rounded, slightly cordate, apically long attenuate, acute, olive green above and reddish brown beneath when dry, glabrous, the margins strongly revolute; 3(–5)-plinerved, the midrib deeply impressed above, raised and conspicuous beneath, the lateral nerves and the veinlets raised and conspicuous above, slightly raised but obscure beneath; petioles subterete, rugose, 2–3.5 mm long, 1–2 mm in diameter, densely puberulent, dark brown. *Inflorescence* viscid, 12–20-flowered, the lowest nodes sterile; rachis long tapering, bluntly angled, minutely striate, glabrous, 5–15 cm long, ca. 1–1.5 mm in diameter, a few globular glands scattered along the rachis; floral bracts prominently veined, often somewhat ribbed, short ciliate apically, oblong or oval elliptic, basally narrowed and rounded, apically rounded or acute, (13–)19–27 mm long, (5–)7–11 mm wide, pink, the margins with sessile, globular glands to 0.2 mm in diameter, (3–)7–12 per side; pedicels subterete, to 8 mm long and 1 mm in diameter, glabrous, with a few globular glands; bracteoles oblong, oblong elliptic or oblanceolate, ca. 25 mm long, 10 mm broad at anthesis, basally rounded, apically broadly rounded, glabrous or marginally short ciliate, located ca. 1 mm below the junction of the pedicel and the calyx, completely enveloping the flowers in bud, clasping the calyx and the corolla at anthesis, with up to 15 globular marginal glands. *Flowers* with the calyx glabrous, 6.5–7.5 mm long, the tube 1.5–2 mm long, 3.5 mm in diameter, cylindric, slightly rugose, basally slightly expanded, globular glands located around margins of the basal expansion and on the tube, the limb campanulate or erect spreading, smooth or slightly ribbed, 5–6 mm long, the lobes triangular, the margins conspicuously glandular callose thickened, the thickenings nearly contiguous at the apex of the lobe, the sinuses obtuse or rounded; corolla ca. 32 mm long, 6 mm in diameter, pink, densely short pilose in the distal $\frac{1}{3}$, the lobes triangular, ca. 2 mm long; stamens 27–28 mm long, the filaments short pilose in the distal $\frac{1}{2}$, alternately 4–4.5 mm and 7.5–8 mm long, the anthers including the tubules alternately ca. 24–24.5 mm and 20 mm long, the thecae 6–7 mm long; style 31–33 mm long. *Berry* not seen.

The leaves of *C. pseudostenophylla* are about nine times longer than wide and are very reminiscent of *C. stenophylla*. Closer examination of the leaves of *C. pseudostenophylla*, however, shows them to be plinerved and apically acute, in contrast to the obscurely pinnately nerved and apically obtuse leaves of *C. stenophylla*. Other characters, especially differences in bracteole size and position also distinguish the two species. The type description was based on immature material. A more recent collection (*Mori & Kallunki 6162*) has resulted in the more detailed description above. *Cavendishia pseudostenophylla* is endemic to western Panama.

BOCAS DEL TORO: Chiriquí Trail, between Criollo and Quebrada Higueron, *Kirkbride & Duke* 779 (MO, NY). VERAGUAS: Along road between Escuela Agrícola Alto Piedra and Río Dos Bocas, ca. 5–8 km from the Escuela, 730–770 m, *Croat* 25938 (MO, NY). 16 km NW of Santa Fé, on road to Calovebora, 300–500 m, *Mori & Kallunki* 6162 (MO, NY). NW of Santa Fé, 8.8 km from Escuela Agrícola Alto Piedra, Pacific side, *Mori & Kallunki* 6168 (MO). Forest near 2nd branch of Río Santa Maria, road from Santa Fé, *Witherspoon & Dressler* 8887 (MO, NY).

18. **Cavendishia pubescens** (H.B.K.) Hemsl., Biol. Centr. Amer., Bot. 2: 273. 1881.

Thibaudia pubescens H.B.K., Nov. Gen. Sp. Pl. 3: 273. 1818. TYPE: Venezuela: near Caracas, *Humboldt & Bonpland* (B, lectotype; not seen, presumably destroyed; P, isoelectotype not seen, photo of isoelectotype, DUKE, F, NY).

Proclesia pubescens (H.B.K.) Klotzsch, Linnaea 24: 33. 1851.

Thibaudia septemneria Willd. ex Walp., Ann. Bot. Syst. 2: 1087. 1852, as syn., nom. illeg. Art. 34.

T. cinnamomifolia Willd. ex Walp., Ann. Bot. Syst. 2: 1087. 1852, as syn., nom. illeg. Art. 34.

Chupalon pubescens (H.B.K.) Kuntze, Rev. Gen. Pl. 2: 383. 1891.

Epiphytic and terrestrial *shrubs*, 1–3 m tall; mature branches subterete or bluntly angled, ridged, moderately short pilose, reddish brown when dry; immature branches and twigs of the new growth flattened and coarsely angled, ridged, densely short pilose with whitish or grayish trichomes ca. 0.5 mm long. *Leaves* elliptic to lanceolate, (5.5–)14–20 cm long, (1.5–)3.5–9 cm broad, basally cuneate, obtuse or rounded, apically long acuminate with a blunt tip or rarely acute, grayish green when dry, densely puberulent on both the surfaces with soft, white trichomes, persistent beneath, often glabrate above; 5(–7)-plinerved, the midrib impressed above and prominently raised beneath, the lateral nerves impressed above but plane distally, raised and prominent beneath, the veinlets plane to slightly raised but obscure on both sides; petioles subterete, rugose, coarsely ridged, (6–)9–15 mm long, 2–3.5 mm in diameter, densely short pilose. *Inflorescence* 7–11-flowered, encircled at the base by densely short-pilose bracts; rachis bluntly angled, striate, rugose, short pilose with persistent, densely white hairs, sometimes fimbriate, 1–2.5(–4.5) cm long, 2–3 mm in diameter, pink, rarely with basal cartilaginous teeth; floral bracts muricate, short pubescent both abaxially and marginally with densely white hairs, elliptic to oblanceolate, basally narrowed, apically rounded, 17–30 mm long, 7–13(–17) mm wide, pale pinkish green or whitish green, usually with small, red, clavate glands abaxially; pedicels bluntly angled, densely short pilose, often fimbriate, 6–14 mm long, 1–1.5 mm in diameter, pink but turning green; bracteoles linear to aristate, rarely oblong, 2–4.5 mm long, to 1 mm wide, densely pubescent and glandular fimbriate. *Flowers* with the calyx pubescent with densely matted white or tan trichomes, glandular fimbriate, 5.5–6.5(–9) mm long, the tube cylindric, 2.5–4 mm long, not basally enlarged, green, the limb campanulate or spreading, (2.5–)3.5 mm long, whitish to pinkish green, the lobes oblong, broadly triangular, obtuse or broadly rounded and apiculate, 1.5–2(–3) mm long, connivent after anthesis, pinkish green, the sinuses obtuse; corolla cylindric or bottle-shaped, slightly constricted basally, narrowed to the throat, (14–)17–19 (–22) mm long, 8 mm in diameter, white or in age tinted with pink, densely short pilose with white or tawny trichomes, the lobes triangular, wide spreading

at anthesis; stamens 11–15.5 mm long, the filaments alternately 2.5–4 mm and 3.5–6 mm long, white, the anthers including the tubules alternately 8–11 mm and 9.5–13 mm long, brownish orange, the thecae 2.5–4 mm long; style glabrous or rarely distally pilose, 13.5–17 mm long. *Berry* densely puberulent, 8–14 mm in diameter.

Cavendishia pubescens is widespread in the Andes of South America from Bolivia to Venezuela. Its most northwestern location is Volcán Chiriquí, Panama, where it is common on the western side of Volcán Chiriquí along the steep roadside slopes northwest of El Hato. It is readily distinguished by pale pinkish to whitish green floral bracts, densely short pilose white corollas, densely pilose to almost wooly calyces, and by persistently puberulent leaves and fruits. The densely matted hairs of the calyx are in themselves enough to distinguish the taxon.

Cavendishia pubescens is closely related to *C. crassifolia*. Several collections from the area between El Hato and Cerro Punta in the vicinity of Volcán Chiriquí suggest the possibility of hybridization between the two species. Such collections are noted below with an asterisk.

CHIRIQUÍ: Road to Cerro Pando, 6 km NE of El Hato, 1840 m, *Correa* 1384 (DUKE). Road to Bambito, beyond the llanos, 1840 m, *Correa & Lazor* 1414 (DUKE, MO). Boquete, *Davidson* 649 (A, F, MO, US). 1.5 mi S of Cerro Punta, 1850 m, *Graham* 288 (GH, MICH). Road NW of El Hato towards Costa Rica, 1690 m, *Luteyn* 853 (DUKE, MO). Pasa Ancho, 1840 m, *Luteyn* 3053* (DUKE), 3054 (DUKE, F, MO, NY). Road NW of El Hato towards Costa Rica, 1690 m, *Luteyn* 3055 (CAS, DUKE, F, GH, LL, MICH, MO, MSU, NY, UC, US, WIS). Road 2 km above Bambito towards Cerro Punta, *Luteyn & Wilbur* 4652* (DUKE, F, GH, MICH, MO, NY, US). Boquete, *Seemann* 1613 (BM, K). Just S of Boquete, *Stern et al.* 1959 (MICH, MO, US). At opening to canyon to Bambito, 1540 m, *Tyson* 5862* (FSU, MO). NE of Cerro Pando, 1500 m, *Wilbur et al.* 11015 (CAS, DUKE, F, FSU, G, GH, LL, MICH, MO, MSU, NY, PMA, UC, US, WIS). Slopes between Nueva Suiza and Bambito, 1690 m, *Wilbur et al.* 11878, 11879* (both DUKE).

19. ***Cavendishia quercina*** A. C. Smith, Contr. U.S. Natl. Herb. 28: 450. 1932.

TYPE: Costa Rica; San José, Cerro Carizia, *Pittier* 14030 (US, holotype; photo of holotype, DUKE, NY; NY, isotype).

Terrestrial and epiphytic *shrubs*, 0.5–2 m tall; stem base to 8 cm in diameter; mature branches terete or subterete, minutely striate, densely puberulent, becoming glabrate, green or often with a tinge of maroon but drying reddish brown; bark grayish or dark brown but drying grayish; immature branches and twigs of the new growth subterete or bluntly angled, sometimes conspicuously striate, usually densely short pilose with grayish or whitish trichomes. *Leaves* oblong, oblong ovate or ovate, 2.5–7.5 cm long, (1–)1.5–3.5 cm wide, basally rounded and subcordate, the sinus often as long as the petiole, leaves hence appearing sessile and somewhat clasping, apically rounded, obtuse, or often subacute in the young leaves or the leaves produced at end of the season, green to metallic blue green when dry, usually densely short pilose on both the surfaces along the leaf margins, the midrib, and the lateral nerves when young, the pubescence usually persistent only on the upper surface; 3–5(–7)-plinerved with the lateral nerves often arising well above the base thus the leaves sometimes appearing pinnate distally; midrib and lateral nerves slightly impressed

above, conspicuously raised beneath, the lateral nerves sometimes slightly raised above, the veinlets impressed, plane or raised above and usually slightly raised but inconspicuous beneath; petioles subterete and often flattened adaxially, often coarsely rugose, (1-)2-4(-6) mm long, 1.5-2 mm in diameter, dark reddish brown when dry, densely short, white puberulent, often becoming glabrate. *Inflorescence* 12-20(-53)-flowered; rachis obtusely angled, frequently muricate, glabrous or densely hirsute, 2-12 cm long, 2-3 mm in diameter at the base, dark pink but turning greenish at anthesis; floral bracts glabrous or marginally short ciliate, smooth or rarely ribbed when dry, commonly marginally glandular fimbriate, the fimbriae often caducous, oblong or oblong elliptic, basally rounded and often somewhat clasping, apically obtuse or rounded, (9.5-)11-18 (-23) mm long, 6-10(-13) mm broad, red; pedicels subterete, often angled, striate and rugose, swollen at both ends, sparsely to densely hirsute or rarely glabrate, (6.5-)10-14(-18) mm long, 0.5-2 mm in diameter, dark pink but turning greenish at anthesis; bracteoles oblong or oblong ovate, 1-3(-5.5) mm long, 0.5-1(-2.5) mm wide, densely marginally glandular fimbriate, glabrous or ciliate or apically short pilose. *Flowers* with the calyx sparsely to densely hirsute, rarely glabrous, (5.5-)6-8(-9) mm long, the tube short cylindric, often 5-ribbed, rugose, 1.5-2.5(-3) mm long, basally enlarged, the enlargement conspicuous and diverging almost at right angles, marginally undulate or only slightly lobed, dark purplish pink but turning greenish at anthesis, the limb cylindric, erect spreading or rarely campanulate, smooth to rugose or sometimes ribbed, (3.5-)4-6(-6.5) mm long including the lobes, red basally and green above but totally red at anthesis, the lobes narrowly or sometimes broadly triangular, 1-2.5 mm long, 1.5-3 mm wide, erect after anthesis, marginally short ciliate and provided along each side of the lobe with 3-5 stout, callose thickened, glandular fimbriae, these rarely fusing into one oblong, concave gland to 0.5 mm long, sinuses broadly rounded and ciliate; corolla slightly constricted and glabrous basally, densely pilose distally, rarely glabrous, (8.5-)11.5-15(-17.5) mm long and 2.5-4.5 mm in diameter, the tube pale pinkish basally, pale green above, the limb and the lobes whitish to pinkish green, the lobes oblong, obtuse, to 2 mm long, erect or slightly spreading at anthesis; stamens 8-15 mm long, the filaments pilose distally, alternately either 2-5 mm or 3-8 mm long, pink basally, white above, the anthers including tubules alternately 5-9.5 mm and 6.5-12 mm long, orange, the thecae 1-4 mm long; style 9-16 mm long. *Berry* 9-10 mm in diameter.

Cavendishia quercina has only been collected once in western Panama. It is scattered and infrequent in Costa Rica. The single collection from Volcán Chiriquí shows no significant variation from the more common Costa Rican material.

CHIRIQUÍ: Valley of upper Río Chiriquí Viejo, White & White 89 (MO).

20. *Cavendishia revoluta* Luteyn, Brittonia 28: 44. 1976. TYPE: Panama; Foster & Kennedy 1906 (DUKE, holotype; photo NY).

Terrestrial *shrub*, glabrous throughout; mature branches terete, striate, minutely rugose, brown to reddish brown when dry; immature branches subterete,

bluntly angled, striate, minutely rugose, light brown when dry. *Leaves* thickly coriaceous, lanceolate to lance ovate, 11–16 cm long, 5–9 cm wide, basally short attenuate, somewhat decurrent, apically acute, somewhat cuspidate, the margins entire and tightly revolute, olive to light greenish brown when dry; 5–7-plinerved, the midrib and the lateral nerves weakly impressed above, sometimes slightly elevated distally, the veinlets raised and conspicuous above, the nerves raised and conspicuous beneath, or with the veinlets sometimes obscure; petioles subterete, sometimes flattened adaxially, rugose 4–10 mm long, 3–5.8 mm in diameter, light olive brown to reddish brown. *Inflorescence* 9–15-flowered; rachis stout, bluntly and coarsely angled, white speckled, ribbed, rugose, 3–4 cm long, 4–5 mm in diameter at the base, cream pink; floral bracts smooth, marginally glandular fimbriate, elliptic, concave, 14–20 mm long, 11–12 mm broad, basally cuneate and truncate, apically rounded; pedicels becoming wider distally, striate, 3.5–7.5 mm long, 1.5–2.5 mm in diameter; bracteoles oblong, marginally glandular fimbriate, 2–3 mm long, about 2 mm broad. *Flowers* with the calyx 9–11 mm long, the tube with short, stout, reddish, glandular fimbriae when immature, cylindric to barrel-shaped, 4–5 mm long, 4.5–5.5 mm in diameter not basally enlarged, the limb cylindric, smooth, 5–6.6 mm long including the lobes, the lobes oblong to broadly triangular, marginally densely glandular fimbriate when young, soon caducous, mature margins dark red, appearing thinner than the main body of the limb, 2–2.5 mm long, 2.5–3 mm broad, the sinuses acute; corolla immature; style persistent, 10–11 mm long. Mature *berry* not seen.

Cavendishia revoluta is endemic to Cerro Jefe, Panama Province. Its most outstanding feature is the overall coarse appearance, exemplified by the thick, hard leaves with tightly revolute margins. According to *Foster & Kennedy 1906*, the leaves have the “distinct smell of wintergreen.” To our knowledge this odor is otherwise found only in *C. quereme* (H.B.K.) Benth. & Hook. from Costa Rica and Colombia.

PANAMÁ: Near top of Cerro Jefe, 900 m, *Foster & Kennedy 1906* (DUKE); *Gentry 5524* (MO, NY). Top of Cerro Jefe, 830–925 m, *Tyson et al. 4391* (FSU, MO).

21. ***Cavendishia santafeënsis*** Luteyn, *Brittonia* 28: 48. 1976. TYPE: Panama; Veraguas, 5 mi W of Santa Fé, *Croat 22986* (MO, holotype; photo of type, DUKE, NY).

Epiphytic *shrub*, glabrous throughout; mature branches and twigs of the new growth subterete, smooth or striate, reddish brown when dry. *Leaves* elliptic, lance elliptic or oblong lanceolate, (8–)10–19 cm long, (2.5–)4.5–6.5 cm wide, basally rounded or narrowly obtuse, apically short acuminate; 3–5-plinerved, the midrib and the lateral nerves impressed above, raised and conspicuous beneath, the outer pair of the lateral nerves anastomosing with the secondary nerves midway up the leaf, the veinlets slightly raised on both the surfaces but conspicuous only above; petioles terete, rugose, ridged, 7–10 mm long, 2–3 mm in diameter, dark brown when dry. *Inflorescence* 9–12-flowered, the lowest few nodes sterile; rachis subterete, stout, 1.5–2.5 cm long, ca. 5 mm in diameter at base; floral bracts thin and translucent when dry, spatulate, apically

rounded and deeply emarginate, 33–45 mm long, 15–20 mm wide at the top, narrowing sharply to 2–6 mm at the base, pale reddish violet, lamina with tiny, red, clavate abaxial glands; pedicels striate, 8–13 mm long, 1–1.5 mm in diameter; bracteoles similar to the floral bracts but 36–44 mm long, 10–12 mm wide at the top, narrowing to ca. 1 mm at the base, conspicuously imbricate distally in bud, the margins without glandular fimbriae or callose thickenings. *Flowers* with the calyx 8–8.5 mm long, the tube cylindric, bluntly 5-angled, 3–3.5 mm long, shallowly enlarged basally, the enlargement undulate but not lobed, the limb cylindric, 5 mm long including the lobes, the lobes narrowly triangular, acute, 3–3.5 mm long, erect after anthesis, marginally glandular callose thickened with oblong glands extending marginally along each side of the lobe, sinuses obtuse; corolla glabrous ca. 42.5 mm long, 7 mm in diameter, white, the lobes 3 mm long, purple; stamens 37–38 mm long, the filaments alternately ca. 2.5 mm and 10.5 mm long, the long filaments puberulent, the anthers including the tubules alternately ca. 36 mm and 28.5 mm long, the thecae 14–15 mm long. *Berry* not seen.

Cavendishia santafeënsis has been collected only three times and much more material is needed before an adequate summation of its characters can be made. It is distinctive, however, in its large bracteoles which reach 35–45 mm in length. These are seemingly the largest of any known *Cavendishia*. The marginally callose-thickened calyx lobes are also distinctive. The species is endemic to the area north of Santa Fé de Veraguas.

VERAGUAS: 5 mi W of Santa Fé on road past the Escuela Agrícola Alto Piedra, Pacific side of divide, 800–1200 m, *Croat* 22986 (MO). Along road past the Escuela Agrícola Alto Piedra, ca. 1000 m, *Luteyn & Wilbur* 4570 (DUKE). 6–7 km W of Santa Fé, road past agricultural school, 1000 m, *Nee* 9724 (DUKE, MO, NY).

22. ***Cavendishia stenophylla*** A. C. Smith, Ann. Missouri Bot. Gard. 27: 327. 1940. TYPE: Panama; *Allen* 1880 (NY, holotype; photo of holotype, DUKE; MO, isotype).—FIG. 5.

Epiphytic and terrestrial *shrubs* ca. 1.5 m tall; stem base to 2 cm in diameter; mature branches terete or obtusely angled, smooth or minutely striate, glabrate, green or brown when fresh but drying tan or reddish brown; immature branches and new twigs terete, obtusely angled or conspicuously flattened, minutely striate, glabrate or densely short pilose. *Leaves* linear, linear lanceolate or elliptic lanceolate, averaging 5–6 times longer than wide, (4.5–)7.5–12(–14.5) cm long, (0.5–)1–2(–2.5) cm wide, basally narrowing, rounded and usually slightly cordate, apically long attenuate to an ultimately blunt tip, reddish to olive brown when dry, glabrous, marginally usually strongly revolute, rarely flat; pinnately nerved, the lowest primary nerves sometimes arcuate to about the middle then anastomosing with the remaining veins forming a collective nerve which extends to the apex, the midrib deeply impressed above and conspicuously raised beneath, the lateral nerves and the veinlets raised and conspicuous above, slightly raised but obscure beneath; petioles subterete, rugose and often longitudinally ribbed, 3.5–6.5(–9) mm long and 1–2.5 mm in diameter, densely short pilose axially, becoming glabrate. *Inflorescence* solitary or rarely two in terminal axils,



FIGURE 5. *Cavendishia stenophylla* A. C. Smith.—A. Habit ($\times \frac{3}{5}$).—B. Stamens, ventral and lateral views ($\times 1\frac{3}{5}$). [After Luteyn 3102 (DUKE).]

8–28-flowered, the lowest 3–8 nodes usually sterile, viscid; rachis conspicuously bluntly angled, minutely striate, glabrous, purple, 5.5–13 cm long, 1–2.5 mm in diameter; floral bracts conspicuously nerved, glabrous, concave or hood-shaped, ovate, 3–6.5 mm long, 2.5–4.5 mm wide, basally rounded and truncate, somewhat auriculate, apically acute or obtuse, the distal $\frac{2}{3}$ of the margin callose thickened, dark purple with greenish tinge; pedicels subterete, striate, apically swollen, glabrous, 11–18(–24) mm long, 0.5–1(–1.5) mm in diameter, dark purple; bracteoles positioned one-third to halfway up the pedicel, conspicuously nerved, glabrous, concave, ovate, 1.5–2.5(–3) mm long, (0.5–)1.5(–3) mm wide, basally continuous (not articulated) with the tissue of the pedicel, apically acute, the distal $\frac{2}{3}$ to $\frac{1}{2}$ glandularly callose thickened, dark purplish green. *Flowers* with the calyx glabrous, (5–)6–7(–8) mm long, sometimes slightly stipitate, the tube cylindric, rugose and ribbed, the surface often muricate, (1.5–)2–3(–4.5) mm long, basally strongly enlarged and deeply lobed, green when immature, dark purple at anthesis but turning greenish after anthesis, the limb cylindric or spreading, rarely campanulate, ribbed, (2–)4–4.5(–5.5) mm long including the lobes, the lobes triangular, 1–1.5(–2) mm long, (1.5–)2–2.5(–3) mm wide, erect after anthesis, completely callose thickened or the margins rarely slightly thinner than the main body, purple, the sinuses obtuse to broadly rounded; corolla slightly constricted basally, narrowed at the throat, outside densely short pubescent, the trichomes usually white, 0.2–0.4 mm long, rarely glabrous, sparsely pilose within, (16–)18–21.5(–22) mm long, 4–8 mm in diameter, pale purple at the constricted base, purple above, the lobes triangular, 1–1.5 mm long, glabrous, reflexed at anthesis often exposing the tips of the anthers; stamens 15.5–19.5 mm long, the filaments alternately 2–3.5 mm and 5–7.5 mm long, white, with medially pilose long filaments and distally pilose short filaments, sometimes glabrous, the anthers including the tubules alternately 12.5–14.5 mm and 15.5–18 mm long, orange, the thecae alternately 4–5.5 mm and 5.5–6.5 mm long; style sigmoid, exserted at anthesis, green. *Berry* glabrous, 12–15 mm in diameter.

Cavendishia stenophylla is endemic to central Panama where it occurs from 700–1,000 m elevation. It is distinguished by the combination of linear leaves with strongly revolute margins, and callose-thickened floral bracts. Linear leaves are found in only one other Central American species, *C. pseudostenophylla*. The basic venation difference between these two species has been mentioned in the discussion of *C. pseudostenophylla*. Callose-thickened floral bracts are unique to *C. stenophylla*.

COCLÉ: Hills N of El Valle, 1000 m, *Allen* 2162 (A). La Mesa, *Allen* 2373 (A, MO). Hills N of El Valle, *Allen* 3551 (MO, US). Slopes of Cerro Pilón near El Valle, 700–900 m, *Duke* 12049(3) (MO). Between Cerro Pilón and El Valle, 700–900 m, *Duke & Dwyer* 13986(1) (MO). El Valle, WEPCOR site, *Kirkbride* 1086 (MO). La Mesa, 850–870 m, *Luteyn* 3102 (DUKE). Trail to Los Llano, 800–850 m, *Luteyn* 3153 (DUKE, NY). Trail to Las Minas, 800–900 m, *Luteyn* 3161 (DUKE, F, MO), 4063 (DUKE, F, MO, US). La Mesa, *Luteyn* 4089 (DUKE, F, MO, NY); *Weaver & Foster* 1635 (DUKE). PANAMÁ: Hills above Campana, 600–800 m, *Allen* 1880 (MO, NY). Cerro Campana forest, 700–900 m, *Allen* 2422 (A); *Blum et al.* 2372 (FSU, MO); *Lewis et al.* 1921 (MO, UC); *Luteyn & Kennedy* 1819 (DUKE); *Luteyn* 3083 (DUKE); *Luteyn* 3191 (DUKE, F, NY); *Luteyn* 3992

(DUKE, F); *McDaniel* 6841 (FSU, MO); *Mori & Bolten* 7676 (MO, NY). Cerro Campana, summit and upper trail, *Witherspoon & Witherspoon* 8477 (MO, NY).

23. ***Cavendishia subfasciculata*** Luteyn, *Brittonia* 28: 50. 1976. TYPE: Panama; Chiriquí, Boquete District, *Luteyn* 3743 (DUKE, holotype; F, GH, LL, MO, NY, PMA, US, isotypes).

Epiphytic *shrub* 7–10 dm tall or terrestrial and 1–3 m tall; stem base to 2.5 cm in diameter; mature branches terete, smooth or minutely striate, glabrous, green but drying tan to reddish brown, usually with a thin, whitish waxy layer over the branches; bark reddish brown; immature branches and twigs of the new growth subterete to bluntly angled, striate, often coarsely ridged, glabrous, reddish brown when dry. *Leaves* lanceolate to lance elliptic, (3–)5–9(–11) cm long, (1–)2–4 cm wide, basally obtuse or rounded, lamina often short decurrent along the petiole, apically short acuminate, often abruptly so, grayish to brownish green when dry, glabrous or often with numerous short trichomes at the base of the midrib adaxially, usually soon glabrate; 5(–7)-plinerved, the midrib plane or more commonly weakly impressed above, the lateral nerves usually raised and conspicuous, rarely weakly impressed above, the veinlets all raised and conspicuous to obscure above, the nerves raised beneath but the veinlets obscure; petioles subterete, usually flattened adaxially, rugose and often coarsely ridged, 7–13 mm long, 1.5–2 mm in diameter, glabrous to weakly pilose adaxially when young, often glabrate when mature. *Inflorescence* (2–)3–6(–9)-flowered, obconic to spherical in bud; rachis flattened, bluntly angled, striate, viscid, glabrous, (0.3–)0.6–1.2(–3.2) cm long, pale green, usually with minute cartilaginous teeth at the base; floral bracts usually translucent when dry, glabrous, smooth or rarely slightly ribbed, usually with minute, red, glandular fimbriae abaxially, oblong to oblanceolate or oblong lanceolate, basally narrowed and somewhat auriculate, apically rounded or obtuse, usually emarginate, or when young with the notch almost completely filled with callose tissue, (1.5–)2–3(–4) cm long, 0.5–1(–2) cm wide, pale green, but suffused with pink along the margins and at the base, drying green; pedicels swollen distally, ridged, glabrous (6–)8–13(–15) mm long and (0.5–)1–1.5 mm in diameter, pale green to cream colored and often suffused with pink, occasionally with cartilaginous teeth at the distal end; bracteoles linear lanceolate, 1–2.5(–3) mm long, 0.5–1 mm wide, apically acuminate and glandular callose thickened on the distal $\frac{1}{2}$ – $\frac{2}{3}$, pale green. *Flowers* with the calyx glabrous, 5–7(–10) mm long, pale green but sometimes suffused with pink, the tube cylindric, weakly rugose, strongly ribbed, (1.5–)2–3(–4) mm long, basally enlarged, deeply lobed, the lobes straight, extending to or just below the pedicel articulation, the limb campanulate to cylindric, smooth or weakly ribbed and minutely papillate when dry, (2.5–)3.5–4.5(–6) mm long including the lobes, the lobes triangular, (0.7–)1–1.5(–2) mm long, 2–3 mm wide, sometimes flaring outward at anthesis, later erect, glandular callose thickened throughout or only for the distal $\frac{2}{3}$, the sinuses obtuse, broadly rounded or flat; corolla slightly constricted basally, narrowed to the throat, often translucent when dry, 20–24(–30) mm long, 5–7 mm in diameter, glabrous or rarely pilose, whitish at the base and the apex, otherwise pinkish violet to rose red, the

lobes triangular or oblong, acute, ca. 1 mm long, reflexed at anthesis, the tips often callose thickened, white with pinkish or violet margins; stamens 19–24.5 mm long, the filaments densely pilose, alternately 2.5–5 mm and 5–10 mm long, pale green, the anthers including tubules alternately 13–20 mm and 17–22 mm long, tawny, the thecae 4.5–7 mm long; style 22–29 mm long, green. *Berry* ca. 9 mm in diameter.

Cavendishia subfasciculata, endemic to western Panama, may be distinguished from *C. megabracteata* by its overall smaller size, by its habit which presents a fuller and more dense appearance, by the green floral bracts as compared with the pinkish or pale purple bracts of *C. megabracteata*, by slightly decurrent leaf bases, and by the leaf venation.

CHIRIQUÍ: Cerro Punta, 2000 m, *Allen* 1535 (MO). Cerro Copete, 2460–2610 m, *Allen* 4860 (G, MO, NY, US). Las Cumbres near Cerro Punta, *Croat* 13701 (DUKE, MO, NY), 26305 (MO); *Croat & Porter* 16082 (MO). Cerro Horqueta, 2000 m, *Hagen & Hagen* 2029 (GH, NY). Bajo Mono, 1500–2000 m, *Luteyn* 3717 (DUKE, F, GH, MO, NY). Boquete District, E side of Cerro Horqueta, 1700–1800 m, *Luteyn* 3743 (DUKE, F, GH, LL, MO, NY, PMA, US); *Luteyn & Wilbur* 4588 (DUKE, NY). Cerro de Lino above Boquete, 1300–1560, *Pittier* 3036 (F, US). VERAGUAS: NW of Santa Fé, below summit of Cerro Tute, *Mori & Kallunki* 5274 (MO, NY).

EXCLUDED SPECIES:

Cavendishia splachnoides A. C. Smith (Contr. U.S. Natl. Herb. 28: 471. 1932) is known only from the type locality in southern Darién Province (Cerro de Garagará, Sambú Basin, 500–974 m). The holotype (*Pittier* 5647, US) and an additional collection (*Pittier* 5659, US) are in such poor condition, however, that it is not possible to include them in this treatment. This species belongs to a complex of lowland taxa extending into Colombia much in need of additional collecting and study.

Cavendishia bomareoides A. C. Smith from Cerro de Garagará, Darién Province was misidentified and must be excluded from the flora of Panama. The Panamanian collection (*Pittier* 5651, US) attributed to this species represents a sterile twig of *C. fusiformis*.

Cavendishia miconioides A. C. Smith is a South American species (Luteyn, 1976) and those specimens from Chiriquí Province which have been identified as *C. miconioides* are a small-leaved form of *C. crassifolia*.

6. DIDONICA

Didonica Luteyn & Wilbur, *Brittonia* 29: 255. 1977. TYPE: *D. pendula* Luteyn & Wilbur.

Epiphytic *shrub*. *Leaves* alternate, estipulate, coriaceous, entire, plinerved. *Inflorescence* of solitary, axillary, pendulous flowers; pedicels 4–6 times as long as the flower and continuous with it; bracts and bracteoles glandular fimbriate. *Flowers* with the hypanthium glabrous, terete; calyx lobes 5, erect; corolla campanulate cylindric, 5–6-parted; stamens 10–12, the filaments distinct, ciliate, narrowing to a connective which extends to the base of the tubules, the anthers finely granular, the tubules slightly shorter than the thecae, somewhat

spreading, dehiscing by oval, latrorse clefts; style glabrous, the stigma peltate, the ovary inferior. *Fruit* unknown.

Didonica is a monotypic, Panamanian endemic characterized by solitary, pendent flowers on an elongate pedicel continuous with the calyx and by anthers dehiscing by oval, latrorse clefts which do not extend to the apex of the tubule.

1. ***Didonica pendula*** Luteyn & Wilbur, *Brittonia* 29: 255. 1977. TYPE: Panama, *Dressler* 5170 (DUKE, holotype; photo of holotype, NY).—FIG. 6.

Epiphytic *shrub* 7–10 dm tall; mature stems subterete, smooth or minutely striate, glabrous or puberulent, dark blackish red when dry; immature stems and twigs of the new growth subterete, striate, glabrous or puberulent, brownish or graying when dry; pseudostipules ca. 2 mm long. *Leaves* lance elliptic to ovate, (4.5)6–9 cm long, (1.5)2–5 cm wide, glabrous, basally rounded to obtuse or shortly cuneate, apically short to long acuminate, entire, green to olive green when dry, glandular fimbriate beneath but fimbriae soon deciduous; 5(–7)-plinerved, the midrib impressed above, thickened and raised for the proximal 1–1.5 cm, elevated beneath, the lateral nerves and the veinlets slightly raised on both the surfaces; petioles subterete, rugose, glabrous, slightly winged laterally, 5–10 mm long, 1.5–2 mm in diameter, dark reddish brown when dry. *Inflorescence* with the rachis 1.5 mm long; pedicels terete, minutely ribbed, glabrous, 15–18 cm long, 0.3–0.5 mm in diameter; floral bract ovate, ca. 1 mm long, marginally glandular fimbriate; bracteoles nearly basal, aristate, ca. 1.5 mm long, marginally glandular fimbriate; hypanthium and calyx glabrous, 10–12 mm long, the tube obconic, muricate, 3.5–5 mm long. *Flowers* with the calyx limb campanulate, conspicuously nerved, 6.5–7 mm long including the lobes, the lobes broadly ovate, apiculate, 2.5 mm long, 5 mm wide at base with acute sinuses; corolla campanulate cylindric, glabrous, ca. 22 mm long, pink, thin and membranous when dry, the lobes broadly ovate, 2.5 mm long, 6 mm wide; stamens ca. 12 mm long, all alike, the filaments ciliate, ca. 4.5 mm long, 2 mm wide at base, narrowing to the connective, the connective extending to the base of the tubules, the anther including the tubules ca. 10 mm long, the thecae 6.8–7.5 mm long, minutely granular, the tubules slightly spreading, 3.0–3.2 mm long, pilose adaxially, dehiscing by oval, latrose clefts 1.5–2 mm long, but the clefts not extending to the apex of the tubule; style glabrous, 16–18 mm long, the stigma peltate. *Fruit* unknown.

In spite of marked morphological variation we have included both of the known collections under the same binomial. The specimen from Coclé (*Allen* 3760) has glabrous twigs, ovate, short-acuminate leaves about 3–5 cm wide and pentamerous flowers. Dressler's specimen from Veraguas (5170) has puberulent twigs, narrowly lanceolate, long acuminate leaves about 2 cm wide and flowers with 5-lobed calyces, 6-lobed corollas and 12 stamens. Additional collections are needed to evaluate these differences and to complete our understanding of the morphology of the species.

COCLÉ: El Valle de Antón, crest of Cerro Pajita, 1100 m, *Allen* 3760 (MO). VERAGUAS: Third branch of Río Santa María, 10–14 km NW of Santa Fé, 650–750 m, *Dressler* 5170 (DUKE).



FIGURE 6. *Didonica pendula* Luteyn & Wilbur. Habit ($\times \frac{1}{2}$). [After Dressler 5170 (DUKE).]

7. DISTERIGMA

Disterigma (Klotzsch) Niedenzu, Bot. Jahrb. Syst. 11: 160, 209. 1889. LECTO-TYPE: *D. empetrifolium* (H.B.K.) Drude.

Vaccinium sect. *Disterigma* Klotzsch, Linnaea 24: 57. 1851.

Vacciniopsis Rusby, Bull. Torrey Bot. Club 20: 433. 1893. TYPE: *V. ovata* Rusby = *Disterigma ovatum* (Rusby) Blake.

Bushy to straggly, terrestrial or epiphytic *shrubs*. *Leaves* alternate, less than 3 cm long, short petiolate, coriaceous, usually obscurely nerved. *Inflorescence* an axillary cluster of 1–6, often subsessile flowers subtended by a few, minute,

subcoriaceous bracts and borne on basally bracteate and always apically bi-bracteolate pedicels. *Flowers* obscurely articulate with the pedicel and embraced by the closely subtending bracteoles; hypanthium campanulate to short cylindric; calyx lobes 4–5, suberect; corolla subcylindric or campanulate cylindric, 4–5-lobed; stamens usually twice as many as the corolla lobes but rarely of the same number as the lobes, the filaments ligulate, the anthers dorsally attached near the base, membranous, prolonged into (1)2 tubules and dehiscing by elongate, elliptical, introrse clefts; style filiform and about as long as the corolla, the stigma truncate; ovary inferior, (3)4–5-celled with numerous ovules and surmounted by a fleshy, mound-like ring. *Berry* coriaceous.

Disterigma is a small genus of about 25 species ranging from the highlands of Guatemala south to Bolivia and east into the Guianas.

Literature:

Smith, A. C. 1933. The genera *Spherospermum* and *Disterigma*. *Brittonia* 1: 203–232.

Wilbur, R. L. 1974. The Central American species of the genus *Disterigma* (Ericaceae: Vaccinieae). *Bull. Torrey Bot. Club* 101:245–249.

- a. Lobes of calyx and corolla 3; corolla deep red; stamens 6 4. *D. trimerum*
- aa. Lobes of calyx and corolla 4; corolla white or pale greenish white; stamens 8.
 - b. Thecae of anthers both emptying into a single tubule about 1.5 mm long; leaves mostly more than 1 cm long and wide and with an apiculus 1–2 mm long 5. *D. utleyorum*
 - bb. Thecae of anthers each emptying into its own tubule (i.e. tubules 2 per anther) 2 mm long or longer; leaves mostly 1 cm or less long and wide and nonapiculate.
 - c. Leaf-blades 2.5 times as long as wide or less and 4 mm wide or wider; calyx lobes eciliate; calyx tube 4-angled in cross-section; corolla tube 6–8 mm long 1. *D. humboldtii*
 - cc. Leaf-blades 3 or more times as long as wide and 2.5–4.5 mm wide; calyx lobes ciliate; calyx tube terete or nearly so in cross-section; corolla tube 4–6 mm long.
 - d. Calyx lobes 2–2.5 mm long; leaves typically widest at or near the middle, usually linear, mostly about 4 times as long as wide; Prov. de Darién 3. *D. panamense*
 - dd. Calyx lobes less than 2 mm long; leaves typically widest above the middle, oblanceolate, mostly about 3 times as long as wide; Prov. de Panamá 2. *D. luteynii*

1. ***Disterigma humboldtii*** (Klotzsch) Niedenzu, *Bot. Jahrb. Syst.* 11: 224. 1889.—FIG. 7.

Vaccinium humboldtii Klotzsch, *Linnaea* 24: 57. 1851. TYPE: S. America, *Humboldt* 2065 (B, holotype, not seen and presumably destroyed).

V. pachyphyllum Hemsl., *Biol. Centr. Amer. Bot.*, 2: 275. 1881. TYPE: Costa Rica, *Endres* 154 (K, holotype, not seen; photo of holotype, NY).

Disterigma pachyphyllum (Hemsl.) Blake, *J. Wash. Acad. Sci.* 16: 365. 1926.

D. mayanum Lundell, *Wrightia* 5: 85. 1975. TYPE: Guatemala; Dept. Baja Verapaz, *Lundell* & *Contreras* 18936 (LL, not seen).

Bushily compact to straggly, terrestrial or epiphytic *shrubs* (2–)5–10(–12) dm tall; branchlets ridged and grooved and indistinctly 3-angled to irregularly 4-angled, typically setose with tawny to chocolate brown trichomes mostly

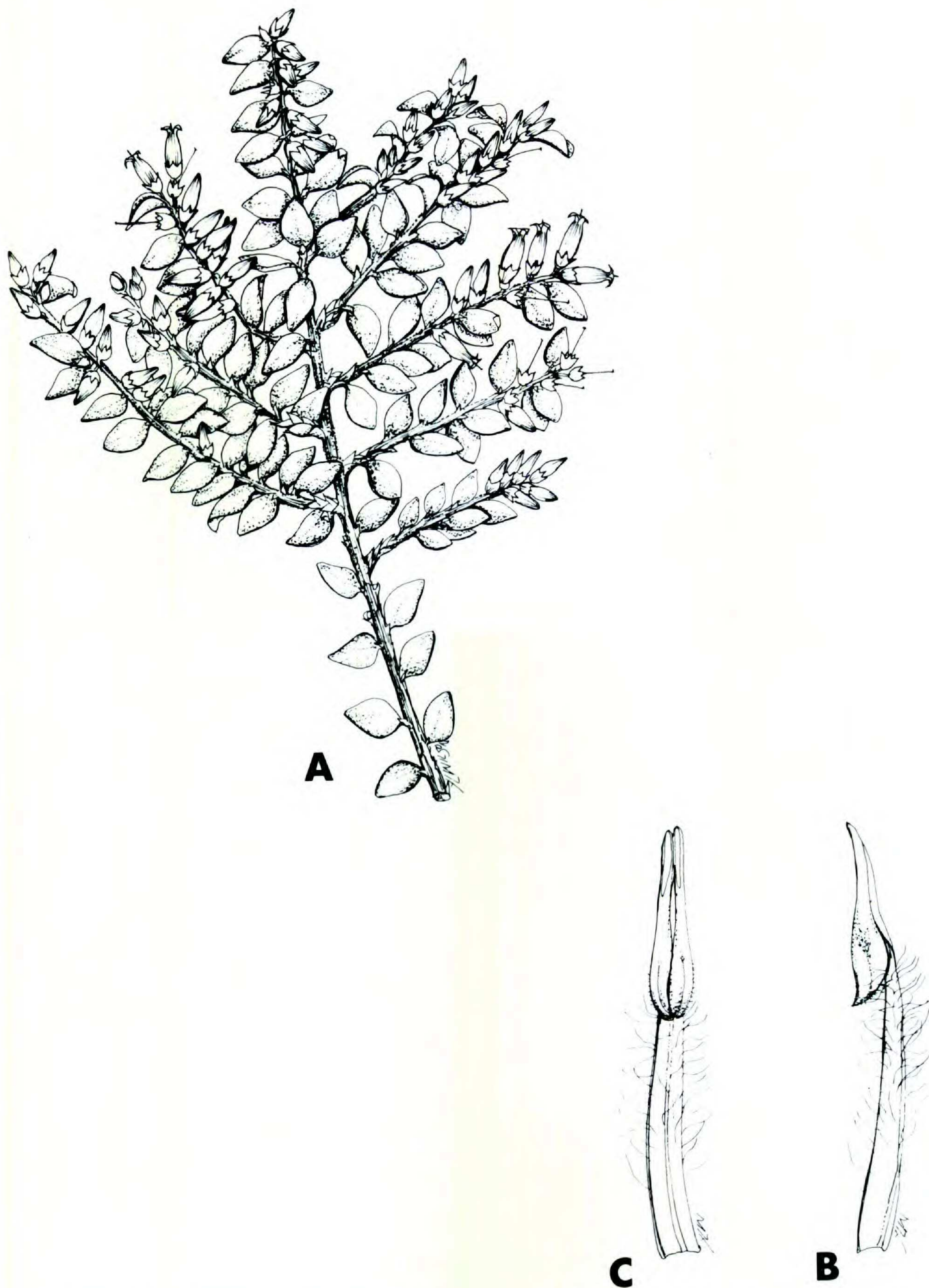


FIGURE 7. *Disterigma humboldtii* (Klotzsch) Niedenzu.—A. Habit ($\times \frac{3}{5}$).—B-C. Stamens.—B. Lateral view ($\times 6$).—C. Ventral view ($\times 6$). [After Wilbur & Luteyn 18803 (DUKE), Costa Rica.]

0.5 to 1.2 mm long or moderately to densely puberulous, becoming glabrate and terete; internodes short on lateral branchlets, usually less than half as long as the nearest leaf, often only 1–2 mm long, but 1–2 times as long as the nearest leaves on fast growing leading shoots. *Leaves* coriaceous, entire, ovate to elliptic to almost orbicular, 6–10(–16) mm long, 4–6(–9) mm wide, apically obtuse to rounded, basally rounded, glabrate or with a sparse scattering of appressed, clavate trichomes 0.2 mm long or less on the lower surface, commonly with a dense but short, apical tuft or marginal cilia, the midvein slightly impressed above, the venation otherwise completely obscure both above and beneath, dark green above and pale green beneath, this distinction persisting when dried; petioles 1(–2) mm long, sparingly to moderately spreading short pubescent. *Inflorescence* of solitary flowers to 2–3 per axil; pedicels ca. 0.5–1(–1.5) mm long; bracts 2–3, basal, broadly clasping, 2–3 times broader than long; bracteoles glabrous, 2, broadly clasping, oblong, truncate, 3–4 mm long and nearly as broad, borne just below and embracing the base of the flower. *Flowers* with the hypanthium 4-angled, campanulate, glabrous, ca. 1 mm long, 1–1.5 mm in diameter; calyx lobes 4, erect to slightly spreading, lance deltoid, acute, 1.5–2.5 mm long, entire and eciliate, 1.5–2.5 mm long, glabrous or sparsely appressed pubescent; corolla white or white and deeply suffused with rose or pink, the tube cylindric, 6–8 mm long, 2–4 mm in diameter, glabrous internally and glabrous to sparingly appressed pilose externally, the lobes 4, erect to horizontally spreading, ca. 1 mm long, deltoid, acute; stamens 8, about as long as the corolla, the filaments 3.5–5 mm long, flattened moderately to densely hyaline setose, the anthers slightly granular, ca. 1.5–2 mm long, each theca tapering into a slender tubule 2.5–3.5 mm long, style glabrous, slightly exerted beyond the corolla lobes.

As is suggested by the description, there is much variability in this species and yet none of it merits formal recognition. *Disterigma humboldtii* is known from Guatemala, Costa Rica, Panama (Bocas del Toro, Chiriquí and Veraguas) and northern South America.

BOCAS DEL TORO: Róbalo Trail, northern slopes of Cerro Horqueta, 6000–7000 ft, *Allen* 4986 (F, MO, US). CHIRIQUÍ: Bajo Mono-Róbalo Trail, W of Cerro Horqueta, 5000–7000 ft, *Allen* 4845 (F, MO, NY, US). Bajo Chorro, Boquete District, 6000 ft, *Davidson* 92 (F, MO). Upland pastures, Las Nubes, 7200 ft, *Luteyn* 3039 (DUKE). Valley of the upper Río Chiriquí Viejo, *White* 25 (MO). Bajo Chorro, 1900 m, *Woodson & Schery* 633 (MO, NY), 684 (MO, NY). VERAGUAS: Cerro Tute, ca. 10 km NW of Santa Fé, on ridgetop in cloud forest above 1000 m, *Mori et al.* 7597 (MO).

2. ***Disterigma luteynii*** Wilbur, Bull. Torrey Bot. Club 101: 248. 1974. TYPE: Panama, Panamá, Cerro Jefe, *Luteyn* 3206 (DUKE, holotype; F, MO, isotypes).

Straggly, scrambling epiphytic *shrub* with branches to 4–6(–10) dm long; branchlets terete, moderately to densely spreading puberulous with hyaline, sordid or tawny trichomes ca. 0.2 mm long; internodes mostly 1–2 mm long but occasionally 3–5 mm. *Leaves* coriaceous, entire, narrowly oblanceolate, or elliptic, 8–12 mm long, 2.5–4.5 mm wide, mostly about 3 times as long as wide,

apically acute in general outline but the actual apex obtuse, gradually tapering basally into the petiole, moderately to densely appressed to spreading pubescent with inconspicuous, fine, hyaline trichomes less than 0.1 mm long on both the surfaces, the lower surface also with a sparse scattering of dark clavate glands, the midvein distinctly impressed above, slightly elevated beneath and the venation otherwise indistinct above and indefinite but pinnately parallel below, dark green above and green below; petioles 1–1.5 mm long, moderately spreading short pubescent with sordid trichomes, conspicuously glaucous. *Inflorescence* of solitary, subsessile flowers; pedicels to 1.2 mm long; bracts 2–3, basal, oblong to ovate, pale green; bracteoles 2, broadly clasping, ovate, broadly rounded, borne just beneath and embracing the flower, outside moderately to densely spreading fine pubescent, glabrous within. *Flowers* with the hypanthium terete, campanulate, glabrous, pale green, 0.5–0.7 mm long, 1.2–1.5 mm in diameter; calyx lobes 4, erect to slightly spreading, deltoid, acute, 1.5–1.7 mm long entire and ciliate, sparsely and very finely pubescent externally; corolla white with pinkish hue, the tube cylindric, 4–5 mm long, 1.8–2.2 mm in diameter, glabrous, the lobes 4, strongly spreading, the recurved tips ca. 1.5 mm long, deltoid, acute with strongly incurved margins; stamens 8, exerted beyond the corolla tube and only a little shorter than the lobes, the filaments white, 2–2.2 mm long, flattened, moderately to densely hyaline setose, the anthers red, minutely granular papillate, ca. 1 mm long, each thecae tapering into a slender tubule ca. 2 mm long; style pale green, glabrous, exerted slightly beyond the corolla lobes.

Disterigma luteynii is only known from the Cerro Jefe region of central Panama.

PANAMÁ: Lowland cloud forest around the summit of Cerro Jefe, ca. 1000 m, *Luteyn* 3206 (DUKE, F, MO). Along the road and at the top of Cerro Jefe, ca. 3000 ft, *Luteyn & Kennedy* 3950 (DUKE, MO, NY). Cloud forest at top of Cerro Jefe, *Mori & Kallunki* 2382 (MO). Premontane rainforest, Cerro Jefe, ca. 1000 m, *Mori & Kallunki* 3610 (MO). Disturbed cloud forest on top of Cerro Jefe, 1000 m, *Nee* 13971 (MO). Cerro Jefe in Clusia forest at 2700–3000 ft, *Tyson et al.* 3266 (SCZ).

3. ***Disterigma panamense*** Standley, Fieldiana Bot. 22: 365. 1940. TYPE: Panama; *Terry* 1564 (F, holotype).

Straggly epiphytic *shrub* 2–10 dm tall; brachlets subterete, irregularly ridged and grooved, moderately to densely spreading pilosulose with hyaline to slightly tawny trichomes mostly 0.3–0.7 mm long; internodes short, mostly less than $\frac{1}{3}$ the length of the nearest leaf and usually 2–7 mm long. *Leaf blades* coriaceous, strongly spreading or merely divergent forming an angle 90° – 45° ; minutely and indistinctly serrulate or entire, typically narrowly linear oblong to elliptic, less commonly shortly and narrowly oblanceolate, mostly 8–12 mm long, 2.5–4 mm wide, typically about 4-times as long as wide, apically acute, basally tapering or somewhat rounded, sparsely and indistinctly appressed pilosulose, especially on the lower surface, becoming glabrate, obscurely and finely short ciliate near the apex but becoming glabrate; venation obscure, neither elevated nor impressed; petioles 1–1.5 mm long, moderately to densely spreading puberulous or short pubescent, the trichomes 0.2–0.5 mm long. *Inflorescences* of solitary,

subsessile flowers; bracts 2–3, basal, broadly clasping, ovate, ciliate, almost as broad as long; bracteoles 2, broadly clasping, ovate, sparsely puberulous, ciliate, 2.5–3.5 mm long, borne just beneath and embracing base of the flower. *Flowers* with the hypanthium terete in cross section, campanulate, glabrous, ca. 1 mm long, 1 mm in diameter; calyx lobes 4, acute, erect, lance ovate, 2–2.5 mm long, entire, conspicuously ciliate with spreading, hyaline trichomes ca. 0.2 mm long, sparsely appressed pilosulose or glabrous; corolla white, glabrous, the tube cylindric, 4–6 mm long, 1.5–2.5 mm in diameter, glabrous, the lobes 4, acute, triangular, erect; stamens equalling the corolla and the style. *Berry* white, thin walled, many seeded.

Disterigma panamense is known only from two collections both made in the mountains of Darién.

DARIÉN: Cuasí-Caná Trail between Cerro Campamiento and La Escaler to “Paramo” east of Tres Bocas, *Kirkbride & Duke 1282* (MO, NY). Caná-Cuasí Trail, 5500 ft, *Terry & Terry 1564* (F).

4. ***Disterigma trimerum*** Wilbur & Luteyn, *Brittonia* 29: 258. 1977. TYPE: Panama, *Wilbur & Luteyn 19321* (DUKE, holotype; CAS, DUKE, F, GH, MICH, MO, NY, PMA, US, isotypes).

Epiphytic or terrestrial, bushy *shrubs* 0.5–1.5(–2) m tall; branchlets sharply ridged and grooved, indistinctly 3-angled to irregularly 4-angled, glabrous, sparingly strigillose or minutely puberulent; mature branches becoming terete, grayish to blackish, conspicuously fissured; internodes $\frac{1}{5}$ – $\frac{3}{5}$ as long as the surrounding leaves. *Leaf blades* coriaceous, entire to obscurely and microscopically serrulate, broadly elliptic to somewhat obovate or spatulate, (0.8–)1.2–1.8 cm long, (4–)6–12 mm wide, apically obtuse to broadly rounded, basally cuneate, glabrous above, beneath evenly but sparingly beset with appressed, amber colored trichomes 0.2–0.3 mm long; midvein and the principal veins slightly elevated above to nearly plane, beneath the midvein and the 1–2 pairs of paralleling principal veins plane or slightly elevated, dark green above, pale green beneath; petioles 3–5 mm long, glabrous, flattened above. *Inflorescence* of solitary, axillary, subsessile flowers; pedicles disarticulating apically, 2–3 mm long; bracteoles subopposite, broadly clasping, semiorbicular, ciliate, 1.5–1.8 mm below the base of the calyx tube, ca. 1.5 mm long, 1.8–2.0 mm wide, scarcely overlapping the base of the hypanthium; bracts 1–3, deltoid to acutely oblong, situated near the base of the pedicel. *Flowers* with the hypanthium terete, short, cylindric, glabrous, ca. 3.5 mm long, 2.0–2.2 mm in diameter; calyx lobes 3, erect, broadly deltoid, acute, ca. 0.5 mm high, entire, eciliate, glabrous; corolla deep red, thinly fleshy, the tube cylindric, abruptly tapering into a basal portion 2.0–2.3 mm long, 1.0–1.4 mm in diameter, the longer portion of the tube 5.0–5.5 mm long, ca. 2.5 mm in diameter, trichomes few, ascendent, 0.1–0.2 mm long, the lobes 3, erect, 1.5–2.0 mm long, 1.0–1.2 mm wide, acute, oblong deltoid; stamens 6, ca. 1 mm shorter than the corolla tube, the free portion of the filaments ca. 2.5 mm long, flattened, glabrous, the anthers granular, 2.5–2.8 mm long, each theca tapering into a slender tubule 2.5–2.8 mm long, dehiscing by an introrse, elongate, oval slit ca. 1.5 mm long; style glabrous, slender, ex-

tending 1.0–1.2 mm beyond the stamens or to the top of the corolla tube. *Berry* at first greenish white turning dark blue.

Except for this species, trimerous flowers are not known in *Disterigma*. The deep red corollas of *D. trimerum* are unlike those of any other Central American representative of the genus. *Disterigma trimerum* is endemic to western Panama.

CHIRIQUÍ: Cloud forest on Caldera-Chiriquicito Trail between Q. Hondo and divide, *Kirkbride & Duke* 939 (DUKE). Heavily forested slopes along W side of Cerro Horqueta, 1700–1800 m, *Luteyn* 3750 (DUKE, NY). Premontane cloud forest along ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn & Wilbur* 4611 (DUKE, NY, US). Cerro Hornitos, 40 km NW of Gualaca, cloud forest dominated by *Quercus*, *Podocarpus* and *Drimys* 2238 m, *Mori & Bolton* 7470 (DUKE, MO). Slopes approaching Cerro Horqueta 6.6 km NNE of Boquete, 1500–1800 m, *Wilbur & Luteyn* 19321 (CAS, DUKE, F, GH, MICH, MO, NY, PMA, US).

5. ***Disterigma utleyorum*** Wilbur & Luteyn, *Brittonia* 29: 259. 1977. TYPE: Costa Rica, *Wilbur* 21706 (DUKE, holotype; CAS, CR, F, GH, LL, MICH, MO, NY, PMA, WIS, etc. isotypes).

Epiphytic *shrub* 2–4.5 dm tall; branchlets subterete to terete, moderately to densely scurfy puberulent; internodes short and mostly $\frac{1}{2}$ – $\frac{2}{3}$ as long as the nearest leaf. *Leaf blades* oblong obovate, somewhat spatulate or rarely oblong elliptic, thick and fleshy, wrinkled when dried, apically obtuse to broadly rounded and often with a pointed apiculus 1–2 mm long, basally broadly cuneate to obtuse, (1.0–)1.5–2.5(–3.0) cm long, (0.7–)1–1.8 cm wide, entire and slightly revolute, both the surfaces minutely or even microscopically puberulent and also with amber colored strigillose trichomes ca. 0.1 mm long; venation with 5 prominently elevated veins radiating from the petiole; petioles 1–2(4) mm long, 1–1.2 mm wide, short puberulent. *Inflorescences* solitary flowers in the axils of the upper leaves, subsessile; pedicels 1–2 mm long, bracts 2, subopposite, broadly oblong to ovate, loosely clasping, minutely appressed puberulous, 1.5–2 mm long, 2–3 mm wide, fused below into a cupule 0.5–1 mm long. *Flowers* with the hypanthium cylindric, 2–3 mm long, pale green, finely and minutely puberulous; calyx rim 1–1.2 mm high, the lobes 4, erect, lanceolate to narrowly triangular, acute, 1.6–2.2 mm long, ca. 1 mm wide at base, minutely puberulous; corolla white, cylindrical or barrel-shaped to somewhat funnelform at maturity, glabrous to sparingly spiculate, the tube 4–5.5 mm long, 3.5–4 mm in diameter, the lobes 4, oblong elliptic, acute, 3.5–5 mm long, about 3 mm wide; stamens 8, ca. 5 mm long, just a little shorter than the corolla tube at anthesis, the filaments white, sparingly ciliate, 1.5–2.5 mm long, the anthers smooth, 2.5–3.5 mm long, the 2 thecae emptying into a single orange tubule 1.5–2.0 mm long which opens by a single, more or less terminal, obliquely introrse, circular pore; style glabrous, 4.8–5.3 mm long, 0.6–0.8 mm in diameter; stigma slightly bilobed. *Berries* reportedly “translucent white.”

This species is known only from recently collected specimens made at low montane elevations from Panama, Costa Rica, Colombia and Ecuador. This species seemingly is always intimately associated with a large colony of ants which vigorously defend their home. The specimens seen by us formed a

picket fence surrounding a large, moist ball of earth and vegetable debris a foot or so in diameter capped by a dense, mat-forming, acrocarpus moss. Details of the commensal relationship between ericad and insect are at present unknown.

VERAGUAS: 5 mi W of Santa Fé on road past Escuela Agrícola Alto Piedra on Pacific side of divide, 800–1200 m, *Liesner* 942 (MO).

8. GAULTHERIA

Gaultheria L., Sp. Pl. 1: 395. 1753; Gen. Pl., ed. 5. 187. 1754. TYPE: *G. procumbens* L.

Chiogenes Salisb., Trans. Hort. Soc. London 2: 94. 1817. TYPE: *C. serpyllifolia* Salisb. = *G. hispidula* (L.) Muhl.

Upright terrestrial or epiphytic *shrubs*, prostrate *undershrubs* or rarely small *trees*. *Leaves* persistent, short petiolate, usually serrate, pinnately veined. *Inflorescences* terminal panicles, axillary racemes or rarely solitary in the axils of the leaves; pedicels clearly articulated or jointed below the flower; bracteoles 2 or several, basal, medial or closely subtending the pedicels. *Flowers* with the calyx (4)5-parted, usually accrescent and becoming somewhat fleshy; corolla campanulate to urceolate, white to pinkish or reddish; stamens (8)10, the filaments distinct, basally expanded, borne on the base of the corolla, the anthers with white tissue on the abaxial side and often with 2, ascendent, terminal awns on each anther sac which open introrsely by a single apical pore; stigma obtuse or truncate, the style straight, the ovary superior or rarely partly inferior, (4)5-locular, ovules 5–10 (or many). *Fruit* a (4)5-valved, loculicidal capsule enclosed by the usually colored, slightly to conspicuously fleshy calyx and thus sometimes appearing superficially berrylike; seeds usually numerous, small, angled, and wingless.

Gaultheria is a genus of 150 species widespread in temperate regions and extending into the montane tropics. It occurs in both northern and southern hemispheres and in both the New and the Old World.

Neither Williams' (1965) attempt to deal with the genus in Guatemala nor ours in southern Central America has satisfactorily resolved the large number of problems associated with the genus in Mexico and Central America; the resolution of problems in the genus in this area clearly demands an intensive study from throughout at least this range.

We find ourselves very sympathetic to the findings of Williams (Fieldiana Bot. 31: 169–172. 1965.) that "... the characters which have been used to segregate species in this genus are not impressive and ... are obviously subject to variation which is almost endless" and "one begins to wonder if perhaps the systematics of the group may not have degenerated to the naming of specimens rather than ... biological units."

- a. Leaves elliptic to lance elliptic, (1–)1.5–2.5(–3.4) cm wide, usually (2.5) 3-times as long as wide 1. *G. gracilis*
- aa. Leaves broadly elliptic to oblong elliptic to oblong, (1.5–)2.5–4.0(–5.5) cm wide, usually less than 2.5-times as long as wide 2. *G. odorata*

1. ***Gaultheria gracilis*** Small, N. Amer. Fl. 29: 77. 1914. TYPE: Costa Rica; La Palma, *Tonduz* 7463 (US, holotype).—FIG. 8.

G. barbata Small, N. Amer. Fl. 29: 77. 1914. TYPE: Costa Rica; Volcán Poás, *Pittier* 2051 (US, holotype).

G. setosa Small, N. Amer. Fl. 29: 77. 1914. TYPE: Panama; *Pittier* 3245 (US, holotype).

G. gracilis var. *intermedia* Suessenguth & Goepfinger, Bot. Jahrb. Syst. 72: 282. 1942. TYPE: Costa Rica, *Kupper* 889 (M). Invalid, Latin diagnosis not provided.

Shrubs 0.4–1.0 m tall, epiphytic or terrestrial; branches terete with brown, grayish or blackish, often fissured bark; branchlets terete, usually moderately to densely strigose with slender, antrorsely appressed, sharply pointed, often hyaline trichomes mostly 0.5–2.5 mm long, occasionally moderately to densely barbate with slender, strongly ascendent to divergently spreading, sharply pointed, golden brown to dark brown trichomes 1–4(–5) mm long, rarely glabrate. *Leaf blades* coriaceous, elliptic to lance elliptic, mostly (3–)4–6(–8.5) cm long, (1–)1.5–2.5(–3.4) cm wide, basally cuneate to rounded, apically acuminate to acute, minutely and indistinctly serrulate, the serrations often tipped by a slender, appressed bristle 1.0–2.2 mm long, above with sparse to plentiful appressed, slender trichomes (0.5–)1.0–2.0 mm long, these often deciduous, their often reddish bases appearing as punctate glands, beneath usually more obviously and densely appressed setose, the slender, golden to reddish brown trichomes (1–)2–3 mm long; venation pinnate, the lateral veins strongly arching towards the apex, the connecting veins forming a conspicuously elevated reticulate pattern, usually less conspicuously so above; petiole subterete or somewhat flattened and grooved adaxially, warty or papillate, drying somewhat wrinkled, short pubescent or glabrate, often strigillose with trichomes 1.0–2.5 mm long, mostly 4–6 mm long, 1.0–1.5 mm in diameter. *Inflorescence* a raceme arising from the axils of the upper leaves; rachis irregularly ridged and grooved or terete, typically moderately to densely puberulent with soft, white trichomes, (2–)3–7(–8) cm long, ca. 1 mm in diameter; floral bracts persistent, membranous to papyriforous, broadly elliptic to spatulate, somewhat cuculate, usually strongly divergent from the rachis, mostly 3–10(–14) mm long, 2–6 mm wide, markedly striate, ciliate and occasionally distally glandular fimbriate, thinly microscopically puberulous on both the surfaces or glabrous, white or greenish white to roseate; pedicels terete, finely striate, usually strongly divergent, but moderately to densely fine puberulous, 5–10(12) mm long, 0.4–0.6 mm in diameter; bracteoles 2, more or less alternate and borne variably in the median half of the pedicel, usually strongly divergent, papyraceous, linear to narrowly oblong, 2.0–4.5 mm long, 0.5–1.0 mm wide, minutely ciliate, creamy or greenish white to roseate. *Flowers* with the calyx sharply demarcated from the pedicel by a groove, the tube smooth, shallowly campanulate, 1.4–2.0 mm long, 2.2–3.5 mm in diameter, broadly rounded basally, the lobes 5, erect, ovate to deltoid, apically acute to acuminate, mostly 2.0–3.0 mm long, basally 1.8–2.5 mm wide, ciliate, the sinuses acute; corolla urceolate to conical, 4–8 mm long, about 3.0–4.0 mm in diameter just above the base, tapering above to 1.8–2.2 mm in diameter just below lobes, greenish, white to deeply roseate; moderately to sparsely beset with hyaline to golden tawny, strigillose trichomes 0.2–0.6 mm long, the lobes oblong to triangu-



FIGURE 8. *Gaultheria gracilis* Small.—A. Habit ($\times 1$).—B–C. Stamens.—B. Lateral view ($\times 11\frac{1}{5}$).—C. Ventral view ($\times 11\frac{1}{5}$). [After Utley & Utley 3718 (DUKE), Costa Rica.]

lar, 1.0–1.5 mm long, slightly spreading to somewhat reflexed at maturity; stamens 10, the filaments distinct, finely papillate, 1.5–2.2 mm long, white, the thecae finely granular, 1.0–1.2 mm long, dehiscing by an introrse terminal cleft, each anther sac terminated by 2 extrorsely deflexed awns ca. 0.5 mm long; stigma truncate, the style persistent, glabrous, 2.5–4 mm long, the ovary 5-celled, subglobose, usually glabrous. *Fruit* a 5-celled capsule 2.5–4 mm high, 3.5–5 mm in diameter.

Within the past six decades five or more additional species have been recognized in Panama and Costa Rica based solely upon differences in type and abundance of the pubescence on both vegetative and floral organs. *Gaultheria setosa* appears to be no more than one extreme of a continuum ranging from glabrous to almost densely strigillose corollas. Much of this morphological range can be found in any given population or from the duplicates collected from a sizable population. Instead of strigose twigs or branchlets, *G. barbata* is characterized by a dense covering of strongly spreading trichomes which give those plants so provided a strikingly different appearance. Plants have been found however which have both types of pubescence although on different branches. Other plants are found which blur the sharp distinction between strigose and hirsute by representing a wide range of intermediate states. In fact *Gaultheria gracilis* var. *intermedia* Suessenguth & Goeppinger was proposed as intermediate between *G. gracilis* and *G. barbata*. *Gaultheria gracilis* is endemic to Costa Rica and western Panama.

CHIRIQUÍ: Lower montane rain forest on W-facing slopes of south flank of Cerro Horqueta, 1940–2000 m, *Cochrane et al.* 6268 (F, MO). Premontane rainforest along ridge to the top of Cerro Horqueta, *Luteyn* 3077 (DUKE, NY). Cerro Pando, ca. 16 km NW of El Hato del Volcán, 2000–2482 m, *Mori & Bolten* 7299 (DUKE, MO). Humid forest around Las Sigüas Camp, S slope of Cerro de la Horqueta, ca. 1700 m, *Pittier* 3245 (US). Southern slopes of Cerro Horqueta N of Boquete, 6400–6600 ft, *Wilbur et al.* 13448 (DUKE, F, MO, NY, PMA). S slopes of Cerro Horqueta N of Boquete, 7000 ft, *Wilbur et al.* 13468 (DUKE, F, GH, MICH, MO, NY, PMA, US).

2. ***Gaultheria odorata* Willd.**, Ges. Naturf. Freunde Berlin Neue Schriften 3: 425. 1801. TYPE: Caracas, Venezuela, *Humboldt* in Herb. Willd. (B, not seen, presumably destroyed).

- G. odorata* var. *costaricensis* Donnell Smith, Bot. Gaz. (Crawfordsville) 20: 292. 1895. TYPE: Costa Rica; Cartago, Estrella, *Cooper* 5841 (US, lectotype; F, MO, NY, US isotypes).
G. costaricensis (Donnell Smith) Small, N. Amer. Fl. 29: 79. 1914.
G. glandulifera Small, N. Amer. Fl. 29: 78. 1914. TYPE: Costa Rica; Volcán Poás, *Donnell Smith* 6639 (NY, holotype; GH, US isotypes).
G. donnellii Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 125. 1934. TYPE: Costa Rica; Laguna de Barba, *Hoffmann* 3 (B, holotype, not seen; fragment of holotype, US).
G. poasana Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 127. 1934. TYPE: Costa Rica; Volcán Poás, *Donnell Smith* 6631 (B, holotype; NY, US isotypes).
G. chiriquensis Camp, Ann. Missouri Bot. Gard. 27: 328. 1940. TYPE: Panama; *Allen* 1542 (NY, holotype; MO, US isotypes).

Shrubs mostly 0.5–1.2(–2.0) m tall, terrestrial or rarely epiphytic; branches terete with reddish, reddish brown or grayish, often fissured bark; branchlets terete, extremely varied as to pubescence, often moderately to densely puberulous, hispid with strongly spreading, bristly trichomes to 5 mm long, these often gland tipped, sometimes glabrate. *Leaf blades* coriaceous, broadly elliptic, oblong elliptic to oblong, mostly (3–)5–9(–11) cm long, (1.5–)2.5–4.0(–5.5) cm wide, basally rounded, often broadly so, sometimes cuneate, rarely cordate, apically acute to rounded, often with an abruptly acute tip, shallowly and often indistinctly serrulate, the serrations commonly tipped when young by slender, caducous, setose bristles 0.8–1.2 mm long, the upper surface often glabrous except

for the inconspicuous puberulence in the grooves of the impressed principal veins, occasionally sparingly to moderately beset with erect to strongly ascendent, usually gland tipped bristles 0.3–0.6 mm long, their former presence marked by a reddish punctation, the lower surface sparingly to moderately beset with ascendent, often gland tipped, reddish brown or golden brown trichomes 0.1–0.8 mm long; venation pinnate, the principal veins impressed above and somewhat elevated beneath, the secondary veins strongly arching towards the apex, tertiary and other connecting veins reticulate, visible on both the surfaces; petioles subterete, somewhat flattened and grooved adaxially, often drying wrinkled, often puberulous especially in the adaxial groove, occasionally sparingly to moderately hispid, the bristly trichomes to 2–3 mm long and occasionally gland tipped, occasionally glabrate, mostly 4–12 mm long, 1.5–3.0 mm in diameter. *Inflorescences* racemes arising from the axils of the upper leaves, often aggregated so as to appear densely paniculate; rachis strongly ridged and grooved to terete, mostly (4–)6–10(–12) cm long, 1.0–1.5 mm in diameter, moderately to densely puberulent but often with additionally sparse to dense gland tipped bristles 0.6–1.2 (–2.0) mm long; floral bracts persistent, papyriforous, elliptic to elliptic oblong, oblanceolate or spatulate, somewhat cucullate, usually strongly divergent from rachis, mostly 5–15(–18) mm long, 3–8(–10) mm wide, conspicuously striate, ciliate and usually glandular fimbriate distally, often moderately to densely but inconspicuously puberulous and glabrescent, occasionally sparingly to densely beset with gland tipped bristles externally, greenish white or stramineous to pinkish or roseate; pedicels terete but finely striate, usually strongly divergent, moderately to densely puberulous, occasionally with gland tipped bristles 0.5–1.0 mm long, mostly (5–)8–12 mm long, ca. 0.5 mm in diameter; bracteoles 2, opposite or subopposite, usually borne medially or in the lower half of the pedicel, typically strongly divergent at anthesis, membranous, linear to narrowly elliptic or lanceolate, mostly 3–6 mm long, 0.6–1.2 mm wide, usually whitish puberulous externally and often internally as well, occasionally with reddish, gland tipped bristles 0.2–0.5 mm long, greenish white, stramineous or roseate. *Flowers* with the calyx sharply delineated from the pedicel by a groove, the tube shallowly campanulate, 1.5–2.0 mm long, 2.5–3.2 mm in diameter, broadly rounded basally, the lobes 5, erect, lance ovate to deltoid, apically acute to acuminate, mostly 2.0–3.5 mm long, basally 2.0–2.8 mm wide, ciliate, externally moderately to densely puberulent, occasionally sparingly to densely beset with gland tipped, hirsute trichomes 0.2–0.5 mm long; corolla pentagonally conical to urceolate, moderately to densely hyaline puberulous and occasionally with appressed to spreading, gland tipped, hirsute bristles 0.3–1.0 mm long, 4–8 mm long, 3.0–4.0 mm in diameter just above the base, tapering above to 2–3 mm in diameter, usually roseate, the lobes oblong to deltoid, acute, 1.2–1.6 mm long, spreading to somewhat reflexed at maturity; stamens 10, the filaments distinct, ciliate and also papillate, ca. 2 mm long, white, the thecae finely granular, 1.0–1.2 mm long, dehiscing by an introrse terminal cleft, each anther sac terminated by 2 extrorsely deflexed awns 0.3–0.5 mm long; stigma truncate, the style persistent, usually short puberulous, 3–4 mm long, the ovary 5-celled, subspherical, usually short pubescent. *Fruit* a 5-celled capsule 3–4 mm high, 3.5–4.5 mm in diameter.

Variation encountered within the *Gaultheria odorata* complex resembles that of the *G. gracilis* complex in that it is largely based on type and distribution of pubescence types, but there is more variation in leaf shape in the *odorata* complex than in the *gracilis* complex. *Gaultheria chiriquensis* Camp with its crispy pilose branchlets and conspicuously cordate leaves is the most distinctive element to be segregated. The names *G. odorata* s.s., *G. costaricensis*, and *G. donnellii* are based on plants which all occur in the same general area as *G. chiriquensis* and intermediate specimens have been seen. For the present it is wisest to recognize *G. odorata* as an extremely polymorphic species ranging from southern Mexico into northern South America.

CHIRIQUÍ: Llanos on slopes of Volcán de Chiriquí along Río Chiriquí Viejo, 1200 m, *Allen 1004* (MO, NY). Llanos del Volcán, 1300 m, *Allen 1542* (MO, NY). Llano del Volcán, 1500–1600 m, *Allen & Fairchild 3462* (US). Summit and SW face of Cerro Copete, 9000 ft, *Allen 4882* (MO, US). Slopes of Las Cumbres near Cerro Punta, *Croat 13757* (DUKE, MO). Lava flow between El Hato and Bambito, *D'Arcy 10027* (MO). Top of peak between Barú and Respinga, 3000 m, *D'Arcy 10085* (MO). Roadside, Potrero Muleto to summit of El Barú, *D'Arcy 10168* (MO). Elfin forest on ridges above Potrero Muleto, W slope of Volcán de Chiriquí, 11 km WNW of Boquete, *Davidse & D'Arcy 10249* (DUKE, MO, NY). Lava flow 3 km NE of El Hato del Volcán at base of Barú, *Davidse & D'Arcy 10347* (DUKE, MO, NY). Bajo Chorro, Boquete District, 5000 ft, *Davidson 391* (MO, US). Potrero Muleto, 10500 ft, *Davidson 1019* (F, US). Exposed rocky summit, Piedro de Lino, 1900 m, *Killip 3574* (US). Llanos outside of El Hato del Volcán, 6000 ft, *Luteyn 3051* (DUKE, NY). Barú, 2900 ft, *McCorkle c158* (FSU, SCZ). Moist summit of Cerro de Lino above Boquete, 1560 m, *Maxon 5210* (US). Elfin forest on E side of Volcán Barú, 3000 m to just below summit, *Mori & Bolten 7429* (DUKE, MO). Lava flow on W slopes of Barú, 1500 m, *Mori & Kallunki 5693* (MO). Trail to summit on western slopes of Volcán de Chiriquí, 2500–3400 m, *Mori & Kallunki 5756* (MO). Savanna 1 mi S of Bambito, 1600 m, *Partch 69-21* (F). Forests of Cerro Lino above Boquete, 1300–1560 m, *Pittier 3032* (NY, US). Near peak, Volcán de Chiriquí, 11200 ft, *Terry 1310* (F). Dry windswept canyon, 8 mi NE of El Volcán, 8100–8400 ft, *Tyson 837* (FSU). Lava flow 5 mi above Volcán, 4900 ft, *Tyson 7293* (PMA). West slope of El Barú, 10000–11000 ft, *Tyson & Loftin 6148* (DUKE). W slope of El Barú above 11000 ft, *Tyson & Loftin 6154* (DUKE, FSU). Lava flow NE of El Hato del Volcán near Aguacate, 1800–1900 m, *Wilbur et al. 10975* (DUKE, MO, NY, PMA). W slopes of Volcán de Chiriquí, 9800 ft, *Wilbur et al. 11028* (DUKE). Lava field 5 mi NE of El Hato del Volcán, *Wilbur et al. 11862* (DUKE, MO). Lava field 4 mi NE of El Hato del Volcán near Río Macho del Monte, 1800 m, *Wilbur et al. 13068* (DUKE, MO, PMA). Rocky arroyo on lava field 4.2 km N of El Hato del Volcán, 1400–1600 m, *Wilbur & Luteyn 19412* (DUKE).

9. LATEROPORA

Lateropora A. C. Smith, Contr. U.S. Natl. Herb. 28: 333. 1932. TYPE: *Lateropora ovata* A. C. Smith.

Terrestrial or epiphytic *shrubs*. *Leaves* alternate, petiolate, pinnately veined, coriaceous. *Inflorescences* axillary, compact, umbelliform or racemose, the stout, short pedicels each subtended by a persistent, ovate bract and bearing basally a pair of subopposite, persistent, ovate bractlets. *Flowers* with the hypanthium clearly disarticulating from the pedicel by a conspicuously delineated groove fringed with apparently glandular, minute trichomes, coriaceous, campanulate; calyx lobes 5, triangular, erect; corolla thick walled, broadly urceolate or squatly campanulate, densely pilose within, the lobes 5, triangular, reflexed; stamens 10, nearly as long as the corolla tube, the filaments distinct, weakly adherent to the base of the corolla, pilose especially near the connective, the anther attached

slightly below the middle, the anther sacs granular, strongly basally incurved with the lower $\frac{1}{3}$ protruding inwardly or even turning upward, spurs and awns lacking, tubules small and rudimentary, the thecae dehiscing by lateral clefts extending from the apex to approximately the base; the base strongly curved; stigma truncate, the style filiform, the ovary inferior, 5-locular. *Fruit* a berry.

Lateropora is a genus of two species known only from Panama.

- a. Calyx lobes 2–3 mm long and 4–5 mm wide basally; corolla lobes ca. 3 mm long and 4.5–5.0 mm wide basally; petioles 5–15 mm long; Chiriquí Province 1. *L. ovata*
- aa. Calyx lobes 1.5–2 mm long and 2.0–2.2 mm wide basally; corolla lobes 1.5–1.8 mm long and 2 mm wide basally; petioles 3–5 mm long; Veraguas Province .. 2. *L. santafeënsis*

1. ***Lateropora ovata*** A. C. Smith, Contr. U.S. Natl. Herb. 28: 334. 1932. TYPE: Panama: *Pittier* 3234 (US, holotype; photo of holotype, DUKE, NY).—FIG. 9.

Epiphytic or terrestrial *shrub*, 2–3 m tall; branches and branchlets subterete, glabrous, striate, thick and widely divergent. *Leaf blades* coriaceous, ovate to broadly elliptic, 6–13 cm long, 4–6(–9) cm wide, glabrate or with appressed, reddish brown, strigillose trichomes 0.2–0.6 mm long, basally cuneate, acute to obtuse apically, entire, pinnately veined, the 3–5 secondary veins arcuate and the veinlets conspicuously reticulate, slightly elevated both above and beneath; petioles glabrous, 0.5–1.5 cm long, 1.5–3 mm in diameter. *Inflorescences* compact axillary, umbelliform racemes, the glabrous, stout peduncle and rachis 12–16 mm long, basally bracteate, the broadly ovate, thick, scale-like, ciliate bracts 4–5 mm long, 3.5–4.5 mm wide subtending the pedicels, the pedicels 3–10 mm long, 2 mm in diameter, bracteoles 2, subopposite, broadly ciliate, keeled, ovate, 3–4 mm long, 4–5 mm wide borne near the base of the pedicel. *Flowers* with the hypanthium disarticulating from the pedicel by a marked groove and with a fringe of glandular trichomes 0.1–0.2 mm long, campanulate, thick walled, 4–5 mm high, 4 mm in diameter, sparingly strigillose with appressed glandular trichomes; the limb glabrous, 1–1.5 mm high, the lobes erect or incurved, broadly triangular, acute, 2–3 mm long, 4–5 mm wide basally, short ciliate; corolla tube broadly cylindric or subglobose, pale greenish white, 6–8 mm long, medially 7–8 mm in diameter, sparsely pubescent outside near the middle with appressed trichomes 0.4–0.6 mm long, the lobes spreading to reflexed, triangular, acute, ca. 3 mm long, 4.5–5 mm wide at the base, densely tangled villous within with white trichomes 0.4–0.7 mm long; stamens 10, the filaments flattened, 3–4 mm long, broadened basally to ca. 1 mm wide, tapering gradually upwards to ca. 0.6 mm, glabrous for about the basal third, strikingly pilose above with trichomes 0.5–1 mm long, the anthers medially attached, conspicuously granular, 3–4 mm long, the tubules submembranous, vestigial to 0.3 mm long, the base strongly incurved, ca. 1 mm long, the thecae dehiscing by a longitudinal slit extending from the apex to the base, basally with a pronounced curve; style ca. 7 mm long.

This little known species has been collected only from the vicinity of Boquete on the slopes of Cerro de la Horqueta. It is apparently restricted to the higher and wettest ridges and slopes.

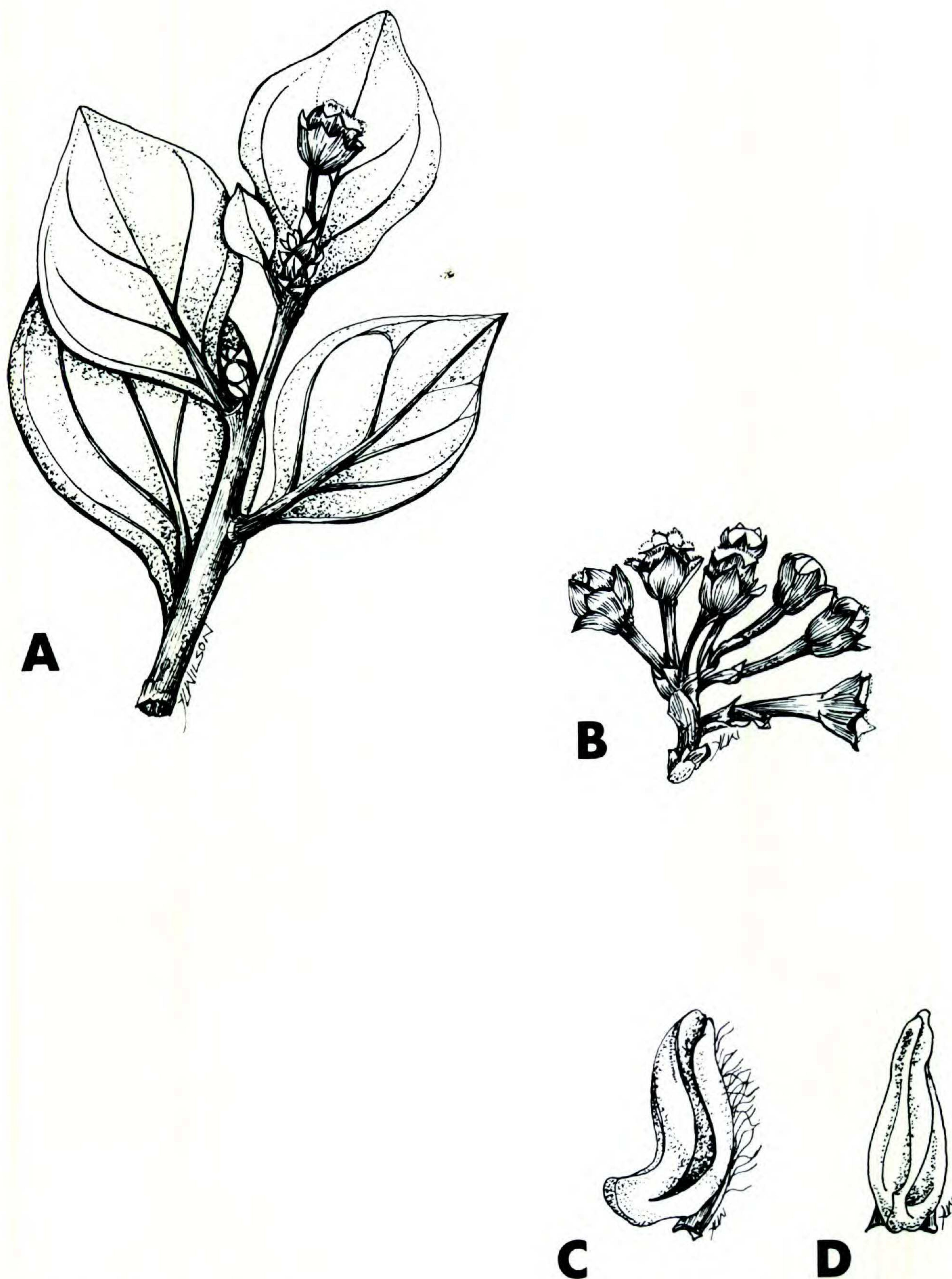


FIGURE 9. *Lateropora ovata* A. C. Smith.—A. Habit ($\times 1\frac{1}{5}$).—B. Inflorescence ($\times 1\frac{1}{5}$).—C-D. Stamens.—C. Lateral view ($\times 5\frac{3}{5}$).—D. Ventral view ($\times 5\frac{3}{5}$). [After Wilbur *et al.* 13485 (DUKE).]

CHIRIQUÍ: Premontane cloud-forest along ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn & Wilbur* 4610 (DUKE, F, US), 4621 (DUKE, MICH, MO, NY). Humid forest, top of Cerro Horqueta, 2268 m, *Pittier* 3234 (US). S slopes of Cerro Horqueta, N of Boquete, 7200 ft, *Wilbur et al.* 13485 (DUKE, MICH, MO). Slopes approaching Cerro Horqueta, 1500–1800 m on trail starting 6.6 km NNE of Boquete, *Wilbur & Luteyn* 19249 (DUKE, F, GH, LL, MICH, MO, NY, PMA, US).

2. ***Lateropora santafeënsis*** Wilbur & Luteyn, *Brittonia* 29: 261. 1977. TYPE: Panama, *Luteyn & Wilbur* 4575 (DUKE, holotype; photo of holotype, NY).

Epiphytic *shrub* 0.5 m tall with stout, glabrous, purplish branchlets and grayish branches. *Leaf blades* coriaceous, elliptic, 3.0–8.5 cm long, 2.0–4.5 cm wide, acutely tapering to both the apex and the base, the margin entire, thickened, slightly revolute, glabrate or with appressed, reddish brown, apparently glandular, strigillose trichomes 0.2–0.3 mm long especially on the lower surfaces, pinnately veined; petioles glabrous, 3–5 mm long, 2.0–3.5 mm in diam. *Inflorescences* axillary, compact, umbelliform racemes 2–3 cm long; peduncle and rachis 8–12 mm long; floral bracts scalelike, ciliate, ovate to suborbicular, somewhat keeled, 2.0–2.2 mm long and about as wide, pedicels stiff, somewhat clavate, glabrous, 5–13 mm long, medially ca. 1 mm in diam., bracteoles 2, subopposite, broadly ovate or suborbicular, ciliate, keeled, appressed, 2.0–2.5 mm long, 1.8–2.2 mm wide, borne on the lower $\frac{1}{4}$ of the pedicel. *Flowers* with the hypanthium glabrous, campanulate, 3–4 mm high, 4–5 mm in diameter, disarticulating from the pedicel by a marked groove often inconspicuously fringed by glandular trichomes 0.1–0.2 mm long; calyx limb glabrous, 0.5–0.7 mm high, the lobes 5, erect, triangular, acute, 1.5–2.0 mm long, 2.0–2.2 mm wide basally, short ciliate; corolla pale greenish, broadly cylindric to urceolate, 4–5 mm long, medially 5–6 mm in diameter, sparingly and inconspicuously strigillose with trichomes 0.1–0.2 mm long, corolla lobes 5, spreading to weakly reflexed, triangular, acute, 1.5–1.8 mm long, 2 mm wide at base, inside densely tangled villous with white trichomes 0.6–1.0 mm long; stamens 10, the filaments flattened, 2.5–3.0 mm long, broadened basally to ca. 1 mm wide, densely pilose distally; anthers attached near the middle just above the basal bend in the thecae, conspicuously granular, ca. 3 mm long, the tubules vestigial, ca. 0.3 mm long, the thecae with a strongly incurved base ca. 1 mm long or $\frac{1}{3}$ the length of the theca, dehiscing by means of a longitudinal slit from the apex to the basal curve.

This species is known only from the holotype.

VERAGUAS: Road beyond Escuela Agrícola Alto Piedra, above Santa Fé and on Pacific Watershed, 800–1000 m, *Luteyn & Wilbur* 4575 (DUKE).

10. LYSICLESIA

- Lysiclesia*** A. C. Smith, *Contr. U.S. Natl. Herb.* 28: 517. 1932. TYPE: *L. caudata* A. C. Smith.

Low, probably epiphytic, *shrubs*. *Leaves* alternate, simple, estipulate, plinnerved, subcoriaceous to coriaceous, entire, shortly petiolate. *Inflorescence* axillary or terminal, racemose; floral bracts solitary at the base of the pedicel, minute, triangular; pedicels bibracteolate near the base. *Flowers* with the

hypanthium articulate with the pedicel, the tube 3-winged, the limb erect, 3-lobed, the lobes 3, erect, membranaceous, greatly enlarged; corolla tubular, membranaceous when dry, the lobes (4–)5, triangular, subacute; stamens 8 or 10, alternately unequal, about $\frac{1}{3}$ the length of the corolla, the filaments distinct or slightly coherent at the base, alternately unequal, anthers basifixed, equal or alternately slightly unequal, the thecae smooth, submembranous, the tubules about the same width as the thecae but shorter, dehiscent by terminal or slightly oblique pores; style filiform, glabrous or distally pilose, the stigma truncate, the ovary inferior. *Fruit* unknown, but presumably a berry.

Lysiclesia may be recognized by the three large calyx lobes and short, alternately unequal stamens with poroid dehiscence. In this last character, *Lysiclesia* resembles *Orthaea* to which it is seemingly most closely related.

Lysiclesia is a neotropical genus with three closely related species, two in Colombia and one in Panama. Each species is known only from its type collection, and therefore, little is known about the variation within the genus.

Literature:

Luteyn, J. L. and R. L. Wilbur. 1977. New genera and species of Ericaceae (Vaccinieae) from Costa Rica and Panama. *Brittonia* 29: 255–276.

Smith, A. C. 1932. The American species of Thibaudieae. *Contr. U.S. Natl. Herb.* 28: 311–547.

1. ***Lysiclesia panamensis*** Luteyn & Wilbur, *Brittonia* 29: 261. 1977. TYPE: Panama, *Mori & Kallunki* 3602 (MO, holotype; DUKE, isotype; photo, NY). —FIG. 10.

Lax *shrub*, almost vinelike; branches terete to bluntly angled, smooth, short pilose, glabrescent, glaucous, reddish brown when dry. *Leaves* ovate elliptic, (2.5–)3.0–3.5 cm long, (1.2–)1.5–2.0 cm wide, basally obtuse or rounded, abruptly short acuminate, apiculate, glabrous, obscurely 3(–5)-plinerved, midrib nearly plane above but raised beneath, the lateral nerves and the veinlets slightly raised and prominent above, obscure beneath. *Petioles* subterete, flattened adaxially, rugose, short pilose, 2.5–3.0 mm long, 1 mm in diameter. *Inflorescence* axillary, racemose, 2–3-flowered; rachis short pilose, bluntly angled, 1.5–2.2 cm long, ca. 1 mm in diameter, with scattered capitate, glandular trichomes ca. 1 mm long; floral bracts lanceolate, 1.5 mm long, ciliate; pedicels subterete, short pilose, 15–17 mm long, ca. 1 mm in diameter, with scattered, capitate, glandular trichomes; bracteoles ovate lanceolate, acuminate, 3–4 mm long, ca. 1.5 mm wide, strongly nerved, ciliate and bearing capitate, glandular trichomes. *Flowers* with the calyx short pilose, 36–37 mm long, reddish brown, the tube obscured by wings which extend slightly below the base, ca. 4.5 mm long, the limb short campanulate, ca. 2 mm long, 3-parted, the lobes triangular, acuminate, basally ca. 10 mm wide, the margins and the lamina with scattered capitate, glandular trichomes; corolla pink, cylindric but narrowing at the throat, the lobes flaring, membranaceous, short pilose outside except at the very base, in-

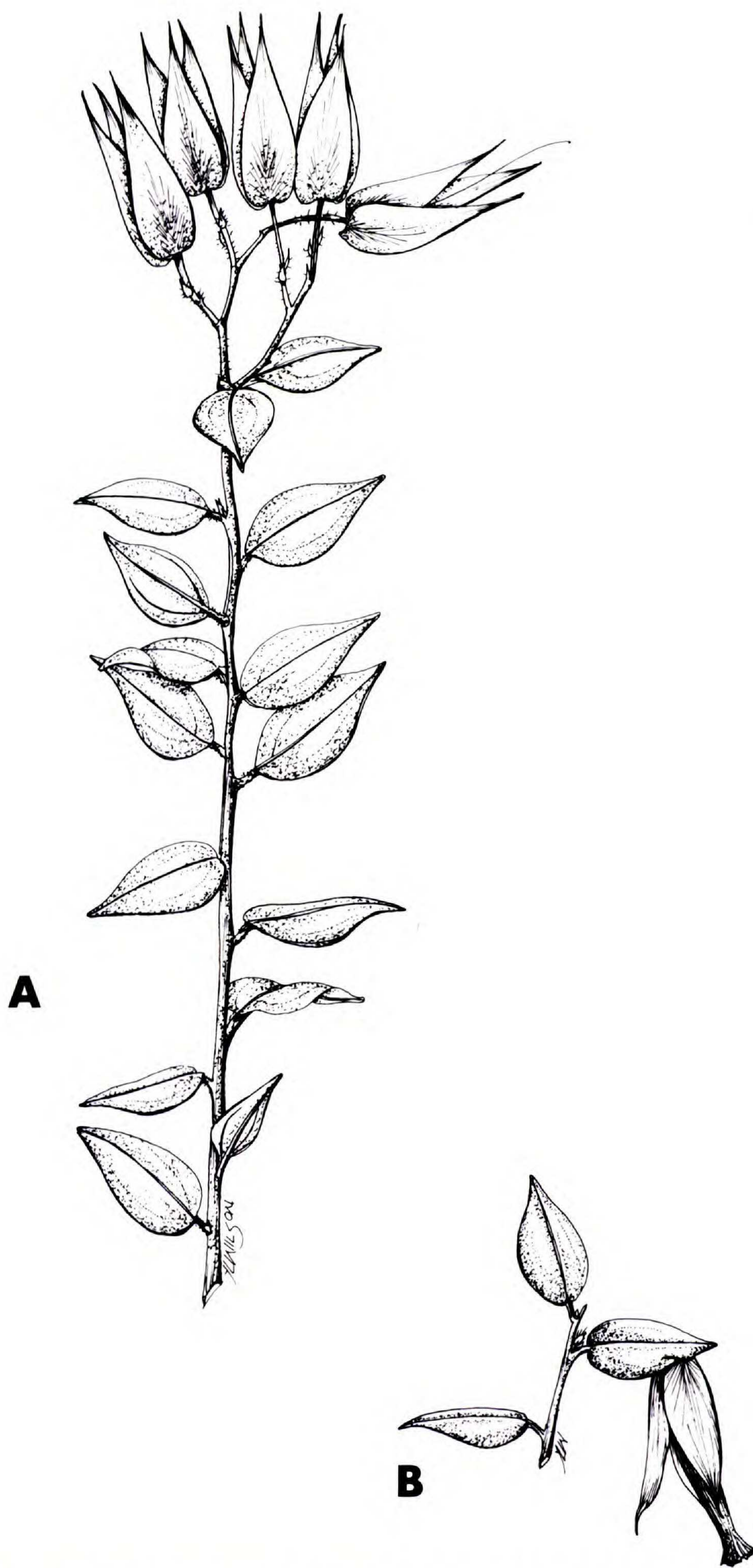


FIGURE 10. *Lysiclesia panamensis* Luteyn & Wilbur.—A. Habit ($\times \frac{7}{10}$).—B. Flower ($\times \frac{7}{10}$). [After Mori & Kallunki 3602 (MO).]

side and at the throat, ca. 35 mm long, the lobes triangular, obtuse, ca. 1 mm long; stamens alternately ca. 10 mm and 12 mm long, the filaments pilose distally, alternately ca. 5 mm and 8.5 mm long, the anthers including tubules slightly unequal, alternately ca. 5 mm and 5.5 mm long, the thecae 2.5–3.0 mm long, the tubules with terminal or, in shorter stamens, slightly oblique pores; style pilose distally, ca. 36 mm long. *Berry* not seen.

This species is known only from a single collection made on Cerro Jefe in Panama province.

PANAMÁ: Cerro Jefe, cloud forest dominated by *Clusia* and *Colpothrinax cookii*, along trail running NE of summit, 1000 m, Mori & Kallunki 3602 (DUKE, MO).

11. MACLEANIA

Macleania Hook., Icon. Pl. 2: pl. 109. 1837. TYPE: *M. floribunda* Hook.

Tyria Klotzsch, Linnaea 24: 21. 1851. TYPE: *T. salapa* (Benth.) Kl. (= *Ceratostema salapa* Benth.)

Straggly to compact, epiphytic or terrestrial *shrubs*. *Leaves* alternate, petiolate, coriaceous, pinnately veined or plinerved. *Inflorescence* axillary or terminal, subfasciculate or racemose with few to many flowers on deciduously bibracteolate pedicels. *Flowers* with the hypanthium articulate with the pedicel, short cylindric or campanulate; calyx limb erect and spreading (3–4)5-lobed, the segments subacute and triangular; corolla subcylindric or elongate urceolate, 5-parted, the lobes triangular and subacute; stamens usually 10, equal, usually about half as long as the corolla, the filaments distinct or connate, dorsally attached to the anthers near their bases, the anthers stout with strongly granular thecae, the tubules about as long as the anther sacs, either laterally connate or fused into a single tubule, rarely completely distinct, opening by elongate, distinct or fused, introrse clefts; style filiform and about as long as the corolla or longer, basally surrounded by an annular or cupuliform disc; the ovary inferior. *Fruit* a berry with numerous, small seeds.

The genus *Macleania* contains approximately 40 species which range from southern Mexico south along the mountainous highlands into Peru.

Literature:

Smith, A. C. 1932. The American species of Thibaudieae. Contr. U.S. Natl. Herb. 28: 311–547.

Yeo, P. F. 1967. Notes on some species of *Macleania* (Ericaceae). Baileya 15: 45–59.

- a. Both anther sacs dehiscing into a single common tubule; filaments distinct or connate.
 - b. Filaments distinct; venation plinerved 1. *M. epiphytica*
 - bb. Filaments connate for most of their length; venation either plinerved or pin-natinerved.
 - c. Calyx wings not extending distally beyond the calyx lobes; venation pli-nerved; bracteoles borne basally on the pedicel 2. *M. insignis*
 - cc. Calyx wings extending distally beyond the calyx lobes and forming per-

- pendicular spurlike appendages; venation pinnatinerved; bracteoles borne medially or more distally on the pedicel 3. *M. pentaptera*
- aa. Each anther sac dehiscing into its own tubule, the tubules usually longitudinally connate; filaments distinct 4. *M. rupestris*

1. ***Macleania epiphytica*** A. C. Smith, Ann. Missouri Bot. Gard. 28: 439. 1941.
TYPE: Panama: Allen 2171 (A, holotype).

Epiphytic *shrub* 0.5–1 m tall, vegetatively glabrous throughout; branchlets terete. *Leaf blades* drying coriaceous, oblong elliptic to ovate, 5–8(–10.5) cm long, 2–3(–5) cm wide, basally rounded or broadly obtuse, apically acute to rounded, entire and with a thickened ridgelike border, 5-plinerved, the veins almost plane to moderately prominent above and slightly elevated beneath, the midvein prominently elevated beneath, the veinlets inconspicuous; petioles thick, drying corrugated, 4–8 mm long. *Inflorescences* axillary, usually in the axils of the upper leaves, fasciculate or obscurely racemose, 2–4-flowered; pedicels stout, 5–11 mm long, bracts minute, triangular to deltoid, 0.5–1.0 mm long, bracteoles 2, papery, ovate to deltoid, acute, 0.6–1.2 mm long borne at or a little above the middle. *Flowers* with the hypanthium articulate with the pedicel, prismatic to cylindric at anthesis, 3–5 mm long and distinctly 5-angled, glabrous; calyx limb suberect and about 2 mm high including the lobes, the lobes 0.5–1 mm long, triangular to broadly deltoid with acute to rounded sinuses; corolla tube thinly fleshy, cylindrical at anthesis, glabrous, 17–18 mm long, basally 3–5 mm in diameter, slightly contracted apically, bright red to scarlet, the lobes 5, deltoid to narrowly oblong, acute, 1.5–3 mm long, dark green, internally whitish puberulent; stamens 10, the filaments membranaceous, ca. 3 mm long, distinct, the sacs 4–4.5 mm long with a single rigid tubule ca. 3 mm long opening by an oval cleft 2.5 mm long; style about as long as the corolla.

This species is known only from the mountains of central Panama.

There is now reasonable question as to the distinction of *M. epiphytica* from *M. insignis*. The primary basis for separating the two species has rested upon the separate filaments of *M. epiphytica* in contrast to the connate filaments of *M. insignis*. However populations and specimens have been encountered in Panama with connate, weakly coherent, and separate filaments. Dark green corolla lobes are often noted as occurring on the specimens with separate filaments but this has not been noted on the more northern specimens of *M. insignis* with connate filaments. It is urged that careful notes be made of the flower colors exhibited by these plants.

COCLÉ: Hills N of El Valle de Antón, 1000 m, Allen 2171 (A). Trail beyond La Mesa towards Los Llanos, N of El Valle de Antón, 800–860 m, Luteyn 3166, 3173a, 4095 (all DUKE). COLÓN: Río Guanche, D'Arcy 9712 (MO). Along road into Santa Rita, E of Agua Clara rain gauge, Kennedy 2742 (MO). Rain forest, Santa Rita Ridge, 5.5–6 mi E of Trans-isthmian Highway, Lewis et al. 5376 (MO). Santa Rita Ridge Road, 14 km from Boyd-Roosevelt Highway, Mori & Kallunki 4920 (MO). PANAMÁ: Primary forest along road from El Llano to Cartí-Tupile, 12 mi from Panamerican Highway, 200–500 m, Croat 22904 (MO). Cerro Campana, 3000 ft, Duke 10726(3) (MO). 19 km above Panamerican Highway, on road from El Llano to Cartí-Tupile, 200–500 m, Kennedy 2551 (MO). Cloud forest, Cerro Campana, 2600–2800 ft, Lewis et al. 1941 (MO). Primary forest along El Llano-Cartí-Tupile road, 12 mi above Panamerican Highway, 200–500 m, Liesner 1219 (DUKE, MO). Road to Cerro

Campana just below Villa Las Minas, 800–900 m, *Luteyn* 3186 (DUKE, MO). Cerro Jefe, 3000 ft, *Luteyn* & *Kennedy* 3964 (DUKE). Cerro Campana cloud forest, 850 m, *Luteyn* 3978 (DUKE). El Llano-Cartí-Tupile Road, 10–12 km N of Interamerican Highway, 500 m, *Luteyn* & *Wilbur* 4665 (DUKE). VERAGUAS: NW of Santa Fé, 4.2 km from Escuela Agrícola Alto de Piedra, *Mori* & *Kallunki* 4825 (MO). Road beyond Escuela Agrícola Alto Piedra above Santa Fé, Pacific watershed, 800–1000 m, *Luteyn* & *Wilbur* 4565 (DUKE, NY).

2. *Macleania insignis* Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 9: 531. 1842. TYPE: Mexico: Veracruz, *Galeotti* 1827 (BR, holotype, not seen; W, isotype, not seen; photo, GH, US).

Thibaudia laurifolia Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 9: 530. 1842. TYPE: Mexico; Oaxaca, *Galleotti* 1814 (BR, holotype not seen; W, isotype not seen; photo, GH, US).

Macleania ovata Klotzsch, Linnaea 24: 20. 1851. TYPE: "in America centrali prope Veraguam," *Warszewicz* (B, holotype, not seen; photo, F).

Macleania cordata var. *linearifolia* Donnell Smith, Bot. Gaz. (Crawfordsville) 16: 12. 1891. TYPE: Guatemala: Pasamala, *Tuerckheim* 1332 (US, holotype; photo, NY).

Macleania linearifolia (Donnell Smith) A. C. Smith, Contr. U.S. Natl. Herb. 28: 368. 1932.

Macleania compacta A. C. Smith, Contr. U.S. Natl. Herb. 28: 369. 1932. TYPE: Mexico; Veracruz; near Jalapa, *Pringle* 7870 (GH, holotype).

Macleania insignis var. *linearifolia* (Donnell Smith) Standley & L. Wms., Fieldiana, Bot. 31: 172. 1965.

Shrubs often epiphytic 0.5–2(–4) m tall; branchlets terete, light to dark brown; bark peeling, puberulous; young twigs glabrous to puberulous. *Leaf blades* ovate to lance ovate or rarely lance oblong to oblong, (2–)3–8(–12) cm long, (1–)1.5–4 cm wide, basally subcordate, rarely rounded, apically obtuse to acute, entire and slightly revolute, glabrous on both surfaces; 3–5(–7)-plinerved with the secondary nerves originating near the base, ascending, the midvein slightly impressed above and elevated beneath; petioles subterete, rugose, glabrous or rarely puberulous, (1–)2–4 mm long. *Inflorescence* axillary, subfasciculate, (1–)2–3-flowered, basally circumscribed by a few, minute, ovate, ciliate bracts 1.5–2 mm long; pedicels rugose, glabrous or rarely puberulous, (4–)8–16 mm long, bracteoles basal, minutely ciliate, triangular, 1–2 mm long. *Flowers* with the hypanthium glabrous or minutely to moderately appressed short pubescent, prismatic, 3–5 mm long, 3–4 mm in diameter, broadly winged from the base to the sinuses, the wings 0.3–0.5 mm wide; calyx limb ascendent to erect, 1.0–1.5 mm long, the lobes 5, apiculate, narrowly triangular to deltoid, (0.4–)0.8–2.0 mm long, the sinuses either flat or acute, more or less contiguous; corolla elongate urceolate or prismatic, (14–)20–25 mm long, 4–5 mm in diameter, contracted at the throat, externally glabrous to slightly puberulous especially distally, distally sparsely to densely villous internally, the lobes acute, spreading, 1.5–3.0 mm long; stamens 10, 8–12 mm long, the filaments dark brown, glabrous, connate 3–5(–7) mm long, the anther sacs 4.0–5.5 mm long, the single, cylindrical-conical tubule 2–3 mm long opening by a broad introrse cleft more than $\frac{1}{2}$ as long as the tubule; style exerted, the stigma peltate.

As interpreted in this account, *Macleania insignis* ranges from the mountains of southern Mexico southward into Panama.

The present treatment is a drastic reduction from the number of species recognized in Smith's (1932) monograph of the genus. The representatives of

this genus with connate filaments in southern Central America have been referred to *M. ovata* Klotzsch. *Macleania ovata* has been generally differentiated from the more northern *M. insignis* by its longer and broader, deltoid calycine lobes which form acute basal sinuses with the adjacent lobes. *Macleania insignis* supposedly had minute calycine lobes less than 1.5 mm long forming a broad, flat sinus between adjacent lobes. There is much greater variability in calycine lobes than was apparent in the relatively few specimens available to Smith, and there is an apparent continuum between the extremes. Hence, there is no way to recognize two taxa based on calycine lobes. Yeo (1967) suggested that *M. ovata* might be best regarded as a geographical subspecies of *M. insignis* but he did not make the combination. The calycine variation does not suggest geographical subspecies since apiculate-lobed plants are found at least as far south as Costa Rica and deltoid, larger lobed plants are to be found in southern Mexico along with the apiculate-lobed plants.

PANAMÁ: Moist upper regions of Cerro Campana, 1000 m, Allen 2406 (A).

3. ***Macleania pentaptera*** Hoerold, Bot. Jahrb. Syst. 42: 299. 1909. TYPE: Ecuador; Sodiro 92/2 (B, not seen; photo, NY).

Epiphytic *shrub*; branchlets terete, glabrous or occasionally sparsely puberulous when young, brownish; root often swollen, tuberous. *Leaf blades* coriaceous, ovate, 8–12 cm long, 4–7 cm wide, glabrous to moderately puberulent beneath, basally strongly cordate or sometimes even amplexicaul, apically rounded or obtuse, rarely subacute, occasionally slightly revolute, pinnately veined, the secondary veins 3 or 4 on each side, arcuately ascending and usually originating near the base; midvein slightly impressed above and prominently elevated beneath, the veins forming a conspicuous reticulum on both sides; petioles thickened, ca. 3 mm long, glabrous or puberulent, rugose. *Inflorescences* axillary, shortly racemose, 3–8-flowered; rachis 0.5–1(–4) cm long; pedicels 12–18 mm long, rugose, glabrous to minutely puberulous; bracts basal, 1–2 mm long; bracteoles 2, medial to supramedial, deciduous, ciliate, deltoid to ovate, 0.5–1 mm long. *Flowers* with the hypanthium obscurely articulate with the pedicel, obconical, glabrous or minutely puberulous distally, 10–13 mm long, 5-winged to the sinuses, the wings fleshy, ca. 0.5 mm broad, projecting above the rim of the calyx to form a coriaceous spur 1–4 mm long; calyx limb dilated, the lobes apiculate, 0.2–0.6 mm long; corolla scarlet to orange red, green distally, cylindric, 13–20 mm long, ca. 5 mm in diameter at thickest point, slightly contracted below the throat, externally glabrous, internally densely pilose distally with trichomes ca. 0.5 mm long, the lobes erect, triangular, acute, ca. 3 mm long, basally 1.5 mm wide, frequently bearing a perpendicular, fleshy, oblong spur; stamens 10, 7–8.5 mm long, about $\frac{1}{2}$ as long as the corolla, the filaments connate, glabrous, 2–3 mm long, the anther sacs 5–7.5 mm long terminated by a single, elongate, conical tubule 3–5.5 mm long opening by an introrse cleft about $\frac{1}{2}$ its length; stigma truncate, the style often slightly exerted from the corolla tube.

The range of this species has only recently been extended to include eastern Panama; it is otherwise known only from Colombia and Ecuador.

DARIÉN: Cloud forest, Cuasí-Caña Trail between Cerro Campamiento and La Escalera to "Paramo," E of Tres Bocas, *Kirkbride & Duke* 1303 (MO). Tres Bocas on the Río Cuasí, *Kirkbride & Duke* 1378 (MO), 1379 (MO, NY).

4. *Macleania rupestris* (H.B.K.) A. C. Smith, *Phytologia* 1: 131. 1935.—FIG. 11.

Thibaudia rupestris H.B.K., *Nov. Gen. Sp. Pl.* 3: 270. 1818. TYPE: Colombia; near Loxa and Alto de Pulla, *Humboldt & Bonpland* (P, holotype, not seen; photo, NY).

Psammisia rupestris (H.B.K.) Klotzsch, *Linnaea* 24: 45. 1851.

P. alpicola Klotzsch, *Linnaea* 24: 45. 1851. TYPE: Colombia, *Moritz* 1349 (B, holotype, not seen; photo, NY).

P. glabra Klotzsch, *Linnaea* 24: 46. 1851. TYPE: "in alpihus Veraguae Americae centralis," *Warszewicz* (B, holotype, not seen; photo, F, GH, NY, US).

P. costaricensis Klotzsch, *Linnaea* 24: 47. 1851. TYPE: "in Americae centralis montibus," *Warszewicz* (B, holotype, not seen; photo, GH, US).

Macleania turrialbana Donn. Sm., *Bot. Gaz. (Crawfordsville)* 27: 339. 1899. TYPE: Costa Rica: Cartago; Volcán Turrialba, *Pittier* 7546 (US, holotype; F, GH, isotypes; photo of holotype, NY).

M. costaricensis (Klotzsch) Hoerold, *Bot. Jahrb. Syst.* 42: 268. 1909.

M. glabra (Klotzsch) Hoerold, *Bot. Jahrb. Syst.* 42: 268. 1909.

M. alpicola (Klotzsch) Hoerold, *Bot. Jahrb. Syst.* 42: 269. 1909.

M. sodiroi Hoerold, *Bot. Jahrb. Syst.* 42: 302. 1909. TYPE: Ecuador.

M. trianae Hoerold, *Bot. Jahrb. Syst.* 42: 303. 1909. TYPE: Colombia.

M. irazuensis Blake, *Proc. Biol. Soc. Wash.* 35: 121. 1922. TYPE: Costa Rica; Cartago, Volcán Irazú, *Popenoe* 1017 (US, holotype).

M. racemosa Cuf., *Arch. Bot. Sist.* 9: 199. 1933. TYPE: Costa Rica; Volcán Poás, *Cufodontis* 717 (W, holotype, not seen, photo F, GH; F, isotype).

Epiphytic or terrestrial *shrub* 0.6–2.0 m high; branchlets subterete, glabrous to rarely moderately puberulent. *Leaf blades* oblong to ovate oblong, rarely elliptic, (2–)4–8(–13.5) cm long, (1.2–)2–5(–7.5) cm wide, basally cuneate to broadly rounded, apically broadly rounded to acute, marginally subentire and slightly revolute, usually glabrous both above and below but occasionally puberulent or spreading short pubescent on the lower surface near the base, occasionally sparsely punctate above; pinnately veined, the midvein slightly impressed above and prominently elevated beneath, the 2–4, arcuate-ascending, secondary veins on each side plane above and prominently elevated beneath, reticulate veinlets also flush above and slightly elevated beneath; petioles rugose, usually glabrous, 4–10 mm long, narrowly winged above. *Inflorescences* axillary near the ends of the branches, racemose, 4–20-flowered, glabrous throughout or occasionally moderately spreading short pubescent; rachis striate, 1–8 cm long; pedicels striate, glabrous to puberulous, reddish, (7–)10–24 mm long; bract single, deltoid or ovate to oblong, often ciliate, 2–5(–7) mm long; bracteoles 2, broadly deltoid to oblong, 1–2(–3) mm long. *Flowers* with the hypanthium short cylindric, ca. 2.5 mm long, 4 mm in diameter, deep maroon; calyx limb flaring, 2–5 mm long including the lobes, the lobes 5, apiculate, ca. 1 mm long; corolla (12–)18–22 mm long, 6 mm in diameter, cylindric urceolate, deep red or pinkish red, the tube contracting at the throat to ca. 3 mm in diameter, the lobes deltoid to oblong, acute, 1.5–2.5 mm long, pale red, pink to white, ciliate; stamens 10, 9–14 mm long, the filaments distinct, glabrous or marginally short pilose distally, 2–4 mm long; the anther sacs basally and apically incurved, 4–7 mm long, the tubules laterally connate throughout, rarely distinct nearly to the

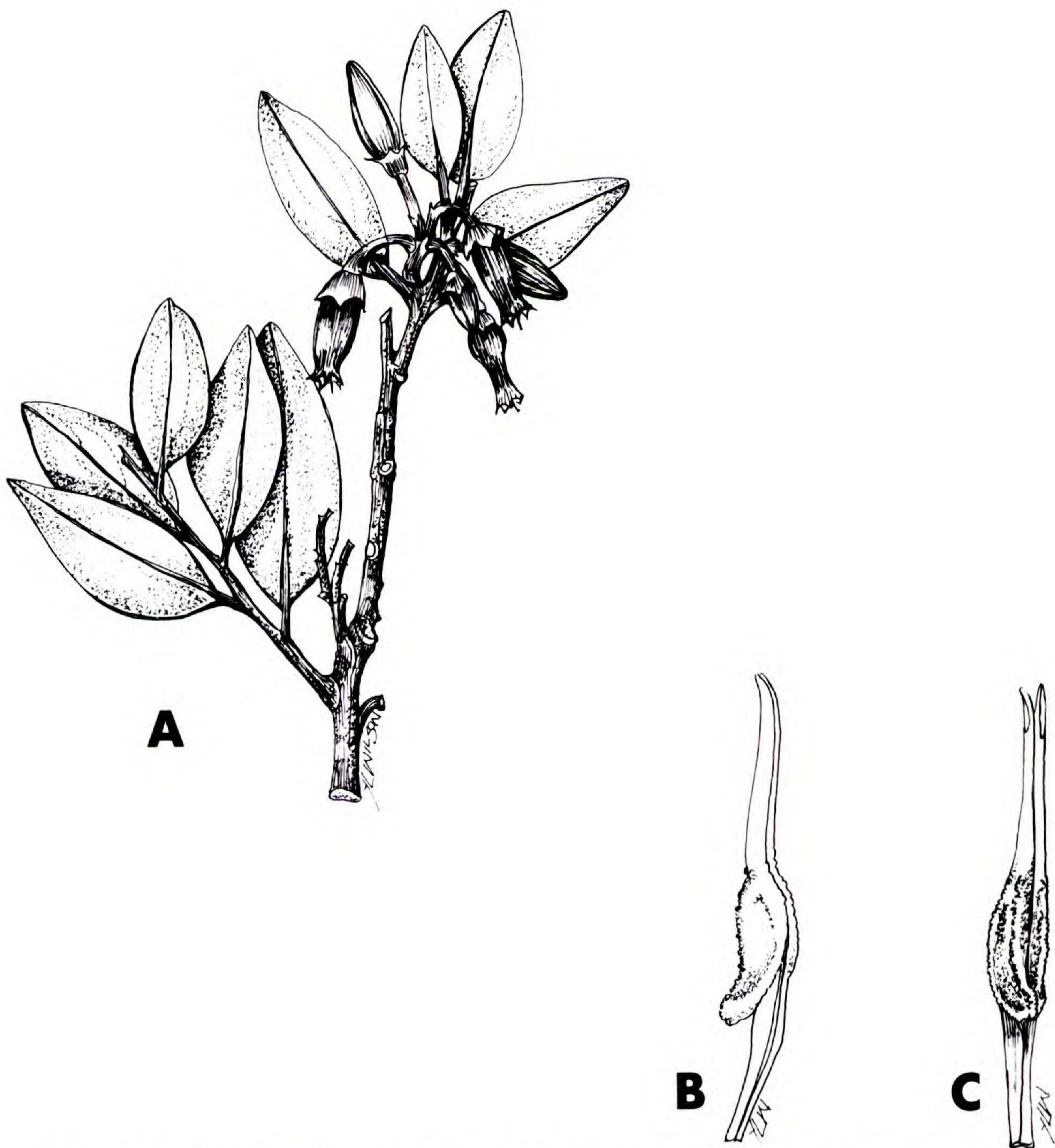


FIGURE 11. *Macleania rupestris* (H.B.K.) A. C. Smith.—A. Habit ($\times 1$).—B–C. Stamens.—B. Lateral view ($\times 5\frac{2}{5}$).—C. Ventral view ($\times 5\frac{2}{5}$). [After Wilbur & Teeri 13077 (DUKE).]

base, rigidly and narrowly cylindric conical, 3.5–6 mm long, opening by elongate, introrse clefts about $\frac{1}{3}$ – $\frac{1}{2}$ the length of the tubule; stigma truncate, the style glabrous. *Berry* dark bluish black.

As interpreted here *Macleania rupestris* occurs in western Nicaragua, Costa Rica and western Panama and from Venezuela and Colombia southward into Peru.

A.C. Smith (1932: p. 378) in his revision of the genus *Macleania* noted a slight morphological distinction which separates the Central American *M. glabra* from the South American *M. nitida* in the sense of Hoerld (= *M. rupestris* (H.B.K.) A.C. Sm.). His key reads as follows.

Tubules slightly shorter than the anther sacs, rarely subequal (South America) *M. rupestris*
 Tubules slightly longer than the anther sacs, rarely subequal (Central America) *M. glabra*

A survey of many specimens from both South and Central America failed to demonstrate any distinction in the ratios of tubules to anther sac between Central and South American specimens. Almost all specimens examined from Costa Rica and Panama had anther sacs longer than the tubules which is contrary to the key. The ample material accumulated in the past forty-five years confirms Smith's suspicion that combining the two supposed taxa is the best course to be followed since no other consistent differences have been detected.

CHIRIQUÍ: Cerro Punta, 2000 m, *Allen 1562* (MO, NY). Summit and SW face of Cerro Copete, 9000 ft, *Allen 4901* (MO, US). Slopes of Las Cumbres near Cerro Punta, *Croat 13702* (DUKE, MO). Wooded slopes on Cerro Horqueta, 1650 m, *Croat 26952* (MO). 10 mi above Boquete on road to Volcán Barú, 2600 m, *Croat 34826* (MO). Eastern slope of Volcán Barú, 8 mi from Boquete, 2300–2400 m, *Croat 34996* (MO). Alto Respinga and above, 2800 m, *D'Arcy 9951* (MO). Potrero Muleto to summit of El Barú, *D'Arcy 10163* (DUKE, MO). Oak forest at 2400 m on E slope of Volcán de Chiriquí, *Davidse & D'Arcy 10217* (DUKE, MO, NY). Elfin forest on ridges above Potrero Muleto on Volcán de Chiriquí, 3000 m, *Davidse & D'Arcy 10258* (DUKE, MO, NY). Bajo Chorro, 6000 ft, *Davidson 158* (A, F, MO, US); *Davidson 609* (F). Volcán de Chiriquí, 9000 ft, *Davidson 975* (A, F, MO). Peak of Volcán de Chiriquí, 11900 ft, *Davidson 1315* (MO). Cerro Respinga on Boquete Trail, 2000–2500 m, *Gentry 5930, 5947* (both DUKE, MO). La Peña Blanca cloud forest, 5500 ft, *Hagen 2001* (A, NY). Cerro Horqueta, 5800 ft, *Lewis et al. 550* (MO). Upland pastures 2–2.5 km E of Cerro Punta, 7150–7200 ft, *Luteyn 3047* (DUKE, F, MO). Premontane cloud forest along ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn & Wilbur 4592* (DUKE). Above timberline on W side of Volcán Barú, 3000 m, *Mori & Bolton 7343* (MO). Oak forest 2.5 km SE of Cerro Punta, *Mori & Kallunki 5675* (MO). Bajo Grande, 1–3 km E of Cerro Punta, 2000–2200 m, *Nee 10027* (DUKE, MO). Volcán Chiriquí, 3000–3371 m, *Pittier 3102* (US). Near peak Volcán de Chiriquí, 11900 ft, *Terry 1315* (A, F). Boquete, El Velo, 6150 ft, *Stern et al. 2001* (US). Boquete, Finca Collins, 5800–6700 ft, *Stern et al. 2024* (US). W slope of El Barú, 6000–7000 ft, *Tyson & Loftin 5948* (DUKE, FSU, MO); *Tyson & Loftin 5958* (DUKE, FSU). W slope of El Barú, 8000–9000 ft, *Tyson & Loftin 6127* (DUKE, FSU). W slope of El Barú, 1000–1100 ft, *Tyson & Loftin 6147* (DUKE, FSU). 5 mi NE El Volcán, 7000 ft, *Tyson 6344* (DUKE). Cerro Punta, 6000 ft, *Tyson 7026* (DUKE). Half-way between Cerro Punta and Bambito, 5600 ft, *Wilbur et al. 10891* (DUKE). W slope of Volcán de Chiriquí, 8600 ft, *Wilbur 11030* (DUKE, MO). Trail between Cerro Punta and Quebrado Bajo Grande, 2000–2100 m, *Wilbur et al. 11896* (DUKE). Steeply cut bank above trail between Bajo Quiel and Bajo Mono 6 mi NW of Boquete, 1450 m, *Wilbur et al. 12015* (DUKE). Trail along Quebrado Grande to top of Paso de Respingo on trail to Boquete, 2100–2400 m, *Wilbur et al. 15117* (DUKE, F, MICH, MO); *Wilbur et al. 15134* (DUKE). Old lava field 4 mi NW of El Hato del Volcán near Río Macho de Monte, 1800 m, *Wilbur & Teeri 13077* (DUKE, MO). Mossy forest E of Guadeloupe along Río Chiriquí Viejo 2 mi NE of Cerro Punta, *Wilbur & Teeri 13101* (DUKE, MO). Quebrado Bajo Grande 2 mi E of Cerro Punta, 6900 ft, *Wilbur & Teeri 13138* (DUKE, MO). Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 817* (MO, NY); *Woodson et al. 976* (A, MO, NY). Loma Larga to summit, Volcán de Chiriquí, 2500–3380 m, *Woodson et al. 1070* (A, MO, NY). Casita Alta to Cerro Copete, 2300–3300 m, *Woodson & Schery 356* (MO). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 381* (MO, NY).

12. MONOTROPA

Monotropa L., Sp. Pl. 1: 387. 1753; Gen. Pl. ed. 5. 183. 1754. LECTOTYPE: *M. uniflora* L.

Hypopitys Hill, Brit. Herb. 221. 1756.

Hypopithys Scopoli, Fl. Carniolica 1: 285. 1771. TYPE: *H. multiflora* Scop.

Fleshy *herbs* lacking chlorophyll, blackening in drying; tawny, reddish or orangey to translucently white; mycorrhizal root parasites (often considered saprophytic); flowering stems nodding at tip but erect in fruit, 1–15 flowers

each borne in the axil of an upper more or less appressed, erose-margined bract, the pedicels recurved, ebracteolate. *Flowers* (3–)4–5(–6)-parted; calyx of 1–5, lanceolate, deciduous, bractlike scales; corolla campanulate, (3–5)6-parted, the petals erect, imbricate, scalelike, distinct, basally saccate and tardily deciduous; stamens 8–10(–12), the filaments distinct, terete, subulate, pubescent, the outer whorl (opposite the petals) shorter than the inner, the anthers short, kidney-shaped, 1-locular at anthesis, opening by a single terminal slit or by ends of a slit which may later open along its entire length; pollen grains single; nectaries of 8–10 paired lobes between the filament bases; stigma funnel-shaped to discoid, obscurely 4–6-lobed, the style columnar, thick, fleshy, the ovary superior, (8)10-lobed, (4–)5(–6) loculate basally with axile placentation, 1-locular above with 4–5, bilobed parietal placentas. *Capsule* globose to ovoid, 8–10-grooved, erect, loculicidally 4–6-valved; seeds numerous, minute, tailed.

Monotropa is a genus of perhaps only two circumpolar species, *M. uniflora* L. and *M. hypopithys* L., both known from Central America. The genus has usually been regarded as a saprophyte or less commonly as a parasite but the studies of Björkman (1960) indicate that it is better considered an achlorophyllous mycotrophyte in which the fungal associate is intermediate between *Monotropa* and its ultimate host.

Literature:

- Björkman, E. 1960. *Monotropa hypopitys* L.—an epiparasite on tree roots. *Physiol. Pl.* (Copenhagen) 13: 308–327.
- Gupton, O. 1962. An analysis of the taxonomic criteria as applied to the genus *Monotropa*. Unpublished Ph.D. thesis. University of North Carolina, Chapel Hill.
- Nowicke, J. W. 1966. Pollen morphology and classification of the Pyrolaceae and Monotropaceae. *Ann. Missouri Bot. Gard.* 53: 213–219.
- Wallace, G. B. 1975. Studies of the Monotropoideae (Ericaceae): taxonomy and distribution. *Wasmann J. Biol.* 33: 1–88.

1. ***Monotropa uniflora* L., Sp. Pl. 1: 387. 1753. TYPE: Virginia, Clayton 245 (LINN, holotype, not seen).—FIG. 12.**

Hypopitys uniflora (L.) Crantz, *Inst. Rei Herb.* 2: 476. 1766.

Monotropa morisoniana Michx., *Fl. Bor. Amer.* 1: 266. 1803. TYPE: Carolina, Michaux (P, not seen).

M. morisoni Pers., *Syn. Pl.* 1: 469. 1805.

M. coccinea Zucc., *Flora* 15: 100. 1832. TYPE: Mexico, Karwinski (M, holotype, not seen).

M. coccinea var. *mexicana* Lange, *Vidensk. Meddel. Naturhist. Dansk. Foren. Kjøbenhavn* 7: 119. 1866.

M. coccinea var. *nicaraguensis* Lange, *Vidensk. Meddel. Naturhist. Dansk Foren. Kjøbenhavn* 7: 119. 1866. Nicaragua, Oersted s.n. (C, holotype; not seen).

M. uniflora var. *coccinea* (Zucc.) Domin, *Abh. Böhm. Ges. Wiss.* 5. 1915.

M. uniflora var. *australis* (H. Andres ex Domin) Domin, *Abh. Böhm. Ges. Wiss.* 6. 1915.

M. brittonii Small, *J. New York Bot. Gard.* 28: 7. 1927. TYPE: Florida; Palm Beach Co., Small et al. 9219 (NY, lectotype).

M. uniflora f. *rosea* Fosberg, *Castanea* 20: 59. 1955. TYPE: Virginia, Limberlost, Shenandoah National Park, Fosberg 36143 (US, holotype).

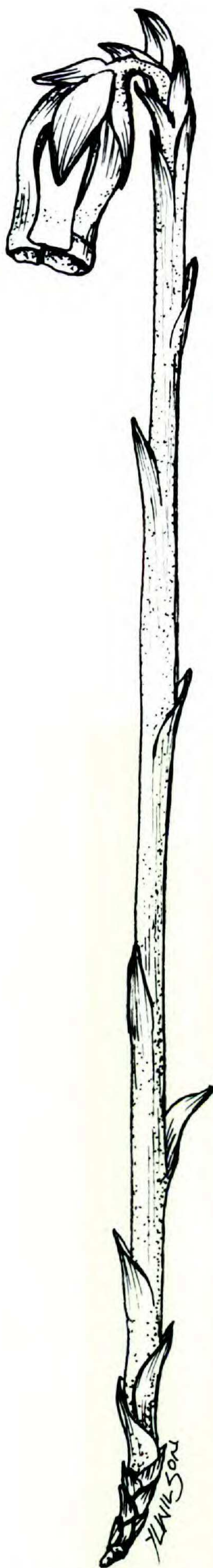


FIGURE 12. *Monotropa uniflora* L. Habit ($\times 1$). [After Mowbray 7.2.63 (DUKE), North Carolina.]

Glabrous, scapose *herbs*, arising from perennial root masses. *Scapes* (5-)13-30 cm tall, 2-5 mm in diameter, terete, somewhat fleshy, striate, bracteate. *Leaves* (bracts) congested both basally and distally, oblong to lanceolate, 6-16(-20) mm long, (2-)3-5(-10) mm wide, apically acute, basally rounded and sessile, the margins entire or somewhat erose. *Flowers* solitary, nodding at anthesis, erect in fruit, perianth 5-merous; sepals 13-16 mm long, 3-7 mm wide, lanceolate, apically obtuse or acute, the margins erose; petals 5-8, 8-16(-20) mm long, (4-)5-15 mm wide, basally saccate, oblong, obovate or spatulate, apically rounded, the margins becoming erose distally; stamens (8-)10(-14), alternately slightly unequal (ca. 1 mm difference in length), the filaments terete, 11-12 mm long, the anthers reniform, appearing peltate, ca. 2 mm in diameter; stigma funnel-shaped, obscurely 5-lobed, 2-6 mm in diameter, the style short, thick, 2-7 mm long, 2-3(-5) mm in diameter; ovary 5-6-locular, globose or ovoid, ca. 7 mm long, 6 mm in diameter. *Capsule* ca. 11 mm long; seeds 1 mm long, spindle-shaped.

Monotropa uniflora is an often clump-forming herb, white to rose pink or carmine in color, but drying black. It is found in the deep shade of humid forest floors in Central America, and has been rarely collected. Nowicke (1966) indicated that the minor differences in shape and size of pollen grains between a single specimen from Labrador and one from Guatemala "suggests that they may be distinct." She treated them respectively as *M. uniflora* L. and *M. coccinea* Zucc., but we are following Wallace's (Wasmann J. Biol. 33: 37-42. 1975) treatment which does not consider *coccinea* as distinct. A larger series of specimens should be examined palynologically before acceptance of Nowicke's suggestion. Wallace's map of the distribution of *M. uniflora* shows the species to range widely through eastern North America and across Canada to the Pacific Northwest. It occurs from Japan and Korea across southern China and through the Himalayas. Its range in Latin America is disjunct from that in eastern North America and also within Latin America since it occurs in Mexico, Central America and Colombia.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley or Río Chiriquí Viejo, 1500-2000 m, *Allen 1500* (MO, NY). El Barú above Boquete, 1200-1800 m, *D'Arcy 9890* (MO). E slopes of Volcán de Chiriquí, WNW of Boquete, oak forest, 2400 m, *Davidse & D'Arcy 10193* (DUKE, MO). Montane forest at lower limit of oaks on steep slope about 9 km by road WNW of Boquete, 1870 m, *Davidse & D'Arcy 10295* (MO).

13. PERNETTYA

Pernettya Gaud., Voy. Freycinet Bot. 454. *tab.* 67. 1826 [1829]. nom. conserv.

TYPE: *P. empetrifolia* (Lam.) Gaud. = *P. pumila* (L.f.) Hook.

Pernetitia Gaud., Ann. Sci. Nat. (Paris) ser. I. 5: 102. 1825. TYPE: *P. empetrifolia* (Lam.) Gaud.

Straggly to densely bushy *shrubs* with depressed, sprawling to erect stems. *Leaves* alternate, persistent, coriaceous or membranaceous, denticulate or serrulate, short petiolate. *Inflorescence* with flowers usually solitary in the axils of the upper leaves or rarely in axillary racemes; pedicels bracteate, nodding,

bibracteolate, indistinctly articulated just beneath the calyx. *Flowers* with the calyx persistent with a short tube and 5 lanceolate to elliptic, acute lobes; corolla tube urceolate, cylindric to ovoid or subglobose, white or white tinged with pink or rose, the lobes 5, less than $\frac{1}{10}$ as long as the corolla tube, reflexed; stamens 10, included well within the corolla, the filaments slightly dilated below, glabrous, the anthers mostly oblong or oval, dehiscent apically by terminal pores, 2 slender awns terminating each anther sac; stigma punctate, the style slender, cylindric, persistent, the ovary superior, 5-loculate, usually subspheroid. *Berry* subglobose to globose, somewhat fleshy and even succulent; seeds numerous, small, angular, compressed.

This is a montane genus of perhaps 15 species. It ranges from Central Mexico south throughout Central America and western South America to southern Argentina and Chile. It also occurs in New Zealand and Tasmania.

Literature:

Camp, W. H. 1939. Studies in the Ericales. IV. Notes on *Chimaphila*, *Gaultheria* and *Pernettya* in Mexico and Adjacent Regions. Bull. Torrey Bot. Club 66: 7-28.

Sleumer, Hermann. 1935. Revision der Gattung *Pernettya* Gaud. Notizbl. Bot. Gard. Berlin-Dahlem, 12: 626-655.

1. ***Pernettya coriacea*** Klotzsch, Linnaea 24: 85. 1851. TYPE: Costa Rica, Warscewicz (B, holotype, not seen).—FIG. 13.

P. setigera Klotzsch, Linnaea 24: 85. 1851. TYPE: Costa Rica; "Vulcán Carthago" [Irazú], Warscewicz (B, holotype, not seen).

P. ciliaris var. *alpina* Donnell Smith, Bot. Gaz. (Crawfordsville) 25: 148. 1898. TYPE: Costa Rica; Cerro de la Muerte, 3100 m, Pittier (Costa Rican herb. no. 10543) (US, holotype). *Gaultheria alpina* (Donnell Smith) Sleumer, Notizblatt Bot. Gart. Berlin-Dahlem 13:207. 1936.

Shrubs erect, bushy, (0.1-)0.2-1.2(-3) m tall; branches moderately to densely short puberulous, moderately or densely strigose or setose on the younger growth but sometimes estrigillose or nonsetose. *Leaves* alternate, persistent, usually with the internodes shorter than the leaves and the leaves strongly overlapping, (6-)12-20(-25) mm long, (3-)5-8(-12) mm wide, coriaceous, narrowly to broadly elliptic or oblong elliptic, glabrous above, beneath glabrous to variably strigillose with short trichomes usually restricted to the midvein but occasionally uniformly dispersed across the surface; margins minutely crenulate serrulate with 6-10 or more teeth on each side, thickened and drying somewhat revolute; petioles mostly 1-4 mm long. Racemes axillary, usually puberulous and often with strigillose trichomes, the bractlets usually several, ovate, oblong to lanceolate, appressed, persistent, 1-3 mm long; pedicels (1-)4-10(-12) mm long. *Flowers* with the calyx persistent, the tube 0.5-1 mm long, the lobes lance ovate to lanceolate, 2-3 mm long, acute, minutely puberulous ciliate and occasionally glandular denticulate, externally often minutely and inconspicuously puberulous especially apically; corolla urceolate, white to lightly roseate tinged, mostly (3.5-)5-7 mm long including the lobes, the lobes erect to reflexed, 0.8-

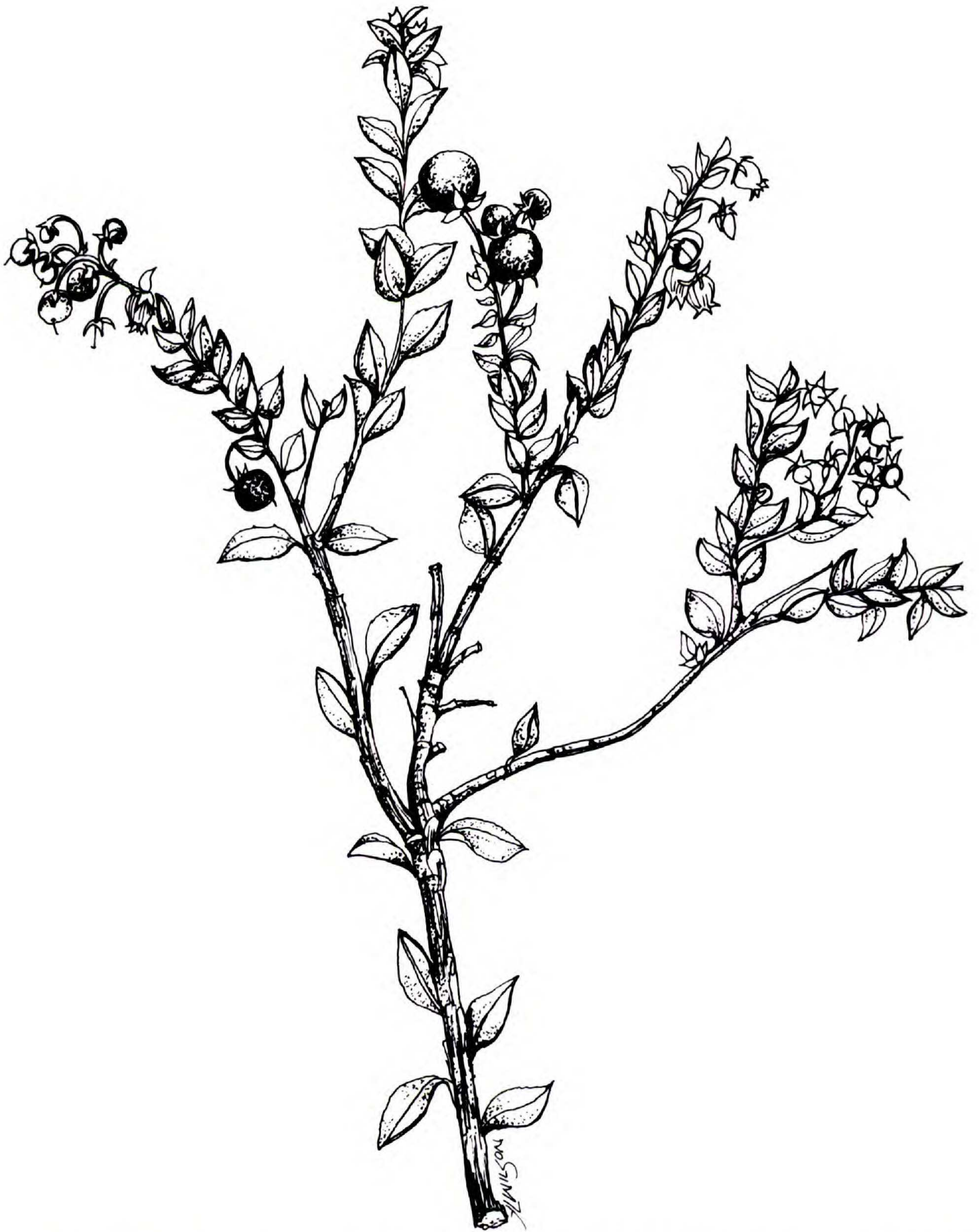


FIGURE 13. *Pernettya coriacea* Klotzsch. Habit ($\times 1$). [After Wilbur & Teeri 13334 (DUKE).]

1.2 mm long, stamens 10, less than $\frac{2}{3}$ as long as the corolla, the filaments minutely granular but glabrous, ca. 2 mm long, dilated, ca. 0.5 mm wide basally, ca. 0.1 mm wide above, the anthers oblong, reddish brown, ca. 1 mm long, dehiscing by a terminal cleft, each sac terminated by 2 slender, straight awns ca. 0.3 mm long; stigma ca. 0.3 mm in diameter glabrous, little wider than the persistent,

glabrous style, the style (1.5)2–2.5 mm long, the ovary globose to subglobose, glabrous to densely short pubescent, ca. 1.5 mm in diameter. *Berry* dark blackish purple, 8–10 mm in diameter, glabrous to densely spreading short pubescent; seeds numerous, compressed, angulate, golden, 0.4–0.6 mm long, the surface shallowly and irregularly reticulate with elongate depressions.

The traditional taxonomic treatment of the polymorphic, highly variable complex to which this species belongs recognized at least one species, *P. ciliata* (Schlect. & Cham.) Small, from Mexico and perhaps Guatemala, a second species, *P. coriacea* Klotzsch, from Costa Rica and western Panama, and a third species, the highly variable *P. prostrata* (Cav.) DC., from the South American Andes. This third species is sometimes attributed also to the higher peaks of the Costa Rican Talamancas. Additional taxa have also been proposed: Camp (1939) recognized six species from Mexico; Standley and Williams (1966) accepted two species for Guatemala and thought there might well be a third. Standley (1938) recognized only one species from Costa Rica in spite of Sleumer's (1935) inclusion, the otherwise South American *P. prostrata* var. *purpurea*. Sleumer was able to separate *P. ciliata* from *P. prostrata* in his key only by geography, admitting that the two species can scarcely be differentiated morphologically. Sleumer provided no descriptions to indicate what tendencies he felt differentiated the two supposed species. Within the extensive range of this variable complex there is much variation in such features as habit, leaf shape, pubescence of leaves, stems and ovaries as well as in the shape and dimensions of the flowers. The resolution of this small but knotty problem will depend upon intensive field study throughout the range of the complex; for the moment we revert to the traditional treatment of the Panamanian representatives.

CHIRIQUÍ: Llanos on slopes of Volcán de Chiriquí along Río Chiriquí Viejo, 1200 m, *Allen* 1006 (F, GH, MO, NY, US), 1300 m, *Allen* 1547 (GH, MO, NY, US). N forested face of Cerro Copete, an E spur of Chiriquí Volcano, 8000–8500 ft, *Allen* 4870 (MO, US). Summit and SW face of Cerro Copete, 9000 ft, *Allen* 4898 (MO, US). Llano del Volcán, *Allen & Fairchild* 3459 (GH, NY, US). Camino a Cerro Punta cerca de 5 kms NW del Hato de Volcán, *Correa* 1379 (DUKE, MO). Volcán Barú, 1 mi from Summit on upper E slopes, 3000 m, *Croat* 34916 (MO). Summit of El Barú, 3225–3447 m, *Croat* 34928 (MO). Lava flow between El Hato and Bambito, *D'Arcy* 10042 (DUKE, MO). Peak between Barú and Respiga, ca. 3000 m, *D'Arcy* 10094 (DUKE, MO). Potrero Muleto to summit of El Barú, *D'Arcy* 10158 (DUKE, MO), *D'Arcy* 10172 (MO). 11 km WNW of Boquete, ridges looking down on Potrero Muleto, *Davidse & D'Arcy* 10237 (DUKE, MO, NY). Lava flow 3 km NE of El Hato del Volcán at base of Volcán de Chiriquí, 1500–1800 m, *Davidse & D'Arcy* 10334 (DUKE, MO, NY). Potrero Muleto, Volcán de Chiriquí, 10400 ft, *Davidson* 1012 (A, F, MO). Lava fields near town of Volcán, 4600 ft, *Duke* 9221 (MO, US). Llanos between El Hato and Cerro Punta, *Ebinger* 794 (MO, US). Lava flow 0.5 mi S of Bambito, *Lazor* 2716 (FSU, SCZ). Open grassland on lava fan 3 mi E of El Volcán, 4500 ft, *Little* 6072 (F, US). Llanos of lava outside El Hato del Volcán on road to Cerro Punta, 6000 ft, *Luteyn* 3052 (DUKE, MO). Summit of Chiriquí Volcano, 3025–3374 m, *Maxon* 5348 (NY). W slopes of Volcán de Chiriquí, 1500 m, *Mori & Kallunki* 5690 (DUKE, MO). Savanna 1 mi S of Bambito, *Partch* 69–25 (MO). Around El Potrero Camp, Chiriquí Volcano, 2800–3000 m, *Pittier* 3078 (GH). Llanos del Volcán, 1120–1200 m, *Seibert* 322 (A). Peak of Volcán de Chiriquí, 11500 ft, *Terry* 1296 (F). Peak, Volcán de Chiriquí, 11900 ft, *Terry* 1334 (A, F). Windswept canyon, 8 mi NE El Volcán, 8100–8400 ft, *Tyson* 835 (FSU, MO). 3 mi N of El Volcán on old lava flow, 5000 ft, *Tyson* 5736 (FSU, MO, SCZ). W slope of El Barú, 6000–7000 ft, *Tyson & Loftin* 5947 (DUKE, FSU). Top of El Barú above 11000 ft, *Tyson & Loftin* 6164, 6165 (both DUKE, FSU); *Tyson & Loftin* 6176 (DUKE, FSU). Cerro Pando, valley of the upper Río Chiriquí Viejo, *White* 17 (MO). Valley of Río Chiriquí Viejo on

llanos near Bambito, *White 45* (NY). Lava flow NE of El Hato del Volcán near Aguacate, 1800–1900 m, *Wilbur et al. 10972* (DUKE, MO, NY, US). Lava field 5 mi NE of El Hato del Volcán, *Wilbur et al. 11864* (DUKE, NY, US). Lava flow between Volcán de Chiriquí and Cerro Aguacate, 6500–7200 ft, *Wilbur & Teeri 13334* (DUKE). Four m NE of El Hato del Volcán, 1950 m, *Wilbur et al. 15415* (DUKE). Lava field 3 km S of Bambito and 4.2 km N of El Hato del Volcán, 1400–1600 m, *Wilbur & Luteyn 19421* (DUKE). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 380, 436* (both GH, MO, NY). Loma Larga to summit, Volcán de Chiriquí, 2500–3380 m, *Woodson et al. 1046, 1093* (both A, MO, NA, NY).

14. PSAMMISIA

Psammisia Klotzsch, *Linnaea* 24: 42. 1851. LECTOTYPE: *P. falcata* (H.B.K.) Kl.

Epiphytic or terrestrial *shrubs*. *Leaves* coriaceous, plinerved or pinnately veined, petiolate. *Inflorescence* axillary or terminal, subfasciculate or racemose with few to many flowers; pedicels deciduous bibracteolate, usually with a sharply delineated disarticulation groove just beneath the flower. *Flower* with the hypanthium short cylindric or campanulate, the limb erect or spreading; calyx lobes (2–4)5, ovate or triangular, apiculate or acute; corolla subcylindric, elongate urceolate or subglobose, 5-lobed, the lobes triangular and subacute; stamens(8)10(12), equal, often nearly as long as the corolla, the filaments distinct or connate, the anthers inserted dorsally near the base, firm, stout with strongly granular thecae, the tubules distinct, $\frac{1}{4}$ to about as long as the anther sacs, opening by elongate introrse clefts, the connectives either all laterally and distally 2-spurred or alternately spurred and spurless (rarely spurs obscure or lacking), the spurs either acute and conspicuous or rounded and not very apparent; style filiform and often exserted. *Fruit* a leathery berry.

This genus consists of approximately 55 species ranging from Costa Rica southward into Bolivia and eastward to French Guiana and Trinidad.

- a. Leaves pinnately veined.
 - b. Leaves 24 cm long or less and 4-times as long as wide or less 2. *P. darienensis*
 - bb. Leaves 25 cm long or more and (5–)6-times as long as wide or more 4. *P. panamensis*
- aa. Leaves plinerved.
 - c. Corolla less than 10 mm long; stamens 4–5 mm long; filaments 1–2.4 mm long, distinct; tubules 1–1.5 mm long; disarticulation groove beneath hypanthium lacking 3. *P. dolichopoda*
 - cc. Corolla 20 mm long or longer; stamens 8 mm long or more; filaments 3 mm long or longer, connate or rarely distinct; tubules 2–4.5 mm long; disarticulation groove beneath hypanthium sharply delineated.
 - d. Rachis of inflorescence 2 cm or longer; anthers including tubules 5.5 mm long or more; calyx lobes ovate or oblong ovate, apiculate, 1–3 mm long 1. *P. columbiensis*
 - dd. Rachis of inflorescence 1 cm long or less; anthers including tubules (5–)7 mm long or less; calyx lobes triangular, acute, ca. 1.5 mm long 5. *P. ramiflora*

1. **Psammisia columbiensis** Hoerold, *Bot. Jahrb. Syst.* 42: 303. 1909. TYPE: Colombia, *Lehmann 4452* (B, holotype, not seen).

Shrub 1–2 m tall, often becoming vinelike with branches scrambling to 7 m; branches terete or subterete, smooth or striate, glabrous or minutely puberulous, reddish or grayish brown when dry. *Leaves* chartaceous or sub-

coriaceous, oblong, elliptic or lance elliptic, 9–14 cm long, 2–4.5 cm broad, basally cuneate and decurrent on the petiole, apically long acuminate, entire, glabrous, 3–5-plinerved, the midrib and the lateral nerves slightly impressed or raised above, conspicuously raised beneath, the veinlets impressed or more frequently raised above, raised and usually conspicuous beneath; petioles 4–6 mm long, 1.5–2 mm in diameter, glabrous, dark reddish brown. *Inflorescence* axillary, racemose, 8–12-flowered; rachis subterete or bluntly angled, glabrous, 2–6 cm long; floral bracts ovate, acute to acuminate, 2–3(–6) mm long, 1–1.5 mm wide, glabrous, marginally scarious; pedicels cylindric, glabrous, 10–20 mm long and 1–1.5 mm in diameter, lengthening to 40; bracteoles 2–3(–4) mm long, similar to the floral bracts. *Flowers* with the hypanthium glabrous, campanulate, slightly rugose, 2–3 mm long, the calyx limb 2–4 mm long including the lobes, the lobes ovate or oblong ovate, apiculate, 1–3 mm long; corolla cylindric, narrowed at the throat, glabrous, 22–27 mm long, 5–7 mm in diameter, the lobes oblong, acute or obtuse, ca. 2–3 mm long; stamens 10, 8–13 mm long, the filaments connate (rarely loosely united in Ecuadorian material) into a distally ciliate tube 3–4 mm long, the connective conspicuously spurred (Panama–Colombia) or seemingly unspurred (Ecuador); the anthers 5.5–11 mm long including the tubules, the thecae slightly glandular, the tubules 2.5–4.5 mm long, dehiscent by clefts 1.5–2 mm long; style 22–29 mm long, exerted at anthesis. *Berry* not seen.

The range of *Psammisia columbiensis* extends from Darién through central and western Colombia to Azuay, Ecuador. The species is characterized by narrow, few-nerved leaves, elongate inflorescences and connate filaments. The few specimens from this wide range show considerable variation and much additional material is needed before a satisfactory circumscription of the species can be made. The material from Panama is incomplete, being vegetatively immature, and lacking an inflorescence, although a single nearly mature flower is found in the packet. This specimen approaches *P. columbiensis* more closely than *P. ramiflora* which is characterized by subfasciculate or short racemose inflorescences and anthers less than 5.5 mm long. *Psammisia ramiflora* is the common species of Costa Rica and central and western Panama. The two species are closely related, however, and are in need of closer study.

DARIÉN: Rain forest, Caná-Cuasí Trail, Chipigana District, 5500 ft, *Terry 1578* (F).

2. ***Psammisia darienensis*** Luteyn & Wilbur,⁵ TYPE: Panama, *Gentry & Mori 14024* (MO, holotype).

Epiphytic *vine*, glabrous throughout except for the filaments; twigs bluntly angled becoming subterete, smooth or slightly striate, brown or grayish brown when dry. *Leaves* subcoriaceous, elliptic to lance elliptic, 16–22 cm long, 6–9

⁵ *Psammisia darienensis* Luteyn & Wilbur, sp. nov. Frutex epiphyticus. Folia elliptica vel lanceolato-elliptica, 16–22 longa et 6–9 cm lata. Racemi axillares, 8–9 floribus. Pedicelli 9–12 mm longi. Calyx 6–6.5 mm longus; lobis 2.5–2.7 mm longis. Corolla cylindrica 7 mm longa. Stamina 10, 6 mm longa; filamentis 1.5 mm longis, pubescentibus; antheris 5.5 mm longis basi rotundatis.

cm wide, basally broadly obtuse or cuneate, shortly decurrent, apically short acuminate, entire, brown when dry, pinnately nerved, the midrib plane or slightly impressed above, conspicuously raised beneath, the 5–7 lateral nerves slightly raised on both the surfaces, anastomosing near the margins, the veinlets slightly raised on both the surfaces; petioles subterete, flattened dorsally, 4–7 mm long, 2 mm in diameter. *Inflorescences* axillary, solitary or paired, racemose, 8–9-flowered; rachis subterete, bluntly angled, 5–7 mm long; floral bracts persistent, coriaceous, ovate lanceolate, acuminate, 2–2.5 mm long, 1.5 mm broad, minutely toothed or glandular fimbriate; pedicels cylindric, striate or ribbed, slightly expanded distally, 9–12 mm long, ca. 0.75 mm in diameter; bracteoles sub-basal, similar to floral bracts but 1.5 mm long, 1 mm broad. *Flowers* slightly beyond anthesis with the hypanthium and the calyx 6–6.5 mm long, the calyx lobes erect, triangular, acute, 2.5–2.7 mm long, the sinuses acute; corolla subcylindric, ca. 7 mm long, 3.5–4 mm in diameter, the lobes triangular, obtuse, 1–1.2 mm long, reflexed at anthesis; stamens 10, conical, 6 mm long, the filaments distinct, ca. 1.5 mm long, 0.75 mm wide, sparsely pilose on the inner surface of the distal half, coarsely ciliate onto the connective margins which become indistinct at the base of the tubules, the connectives neither spurred nor callose thickened, the anthers ca. 5.5 mm long including the tubules, the thecae weakly granular, rounded and broadest at the base, not incurved, the tubules straight, 2–2.3 mm long, dehiscing the length of the tubules by an elongate cleft; style not seen. *Berry* reportedly turning red.

This new species is most closely related to *Psammisia idalima* A. C. Smith which is known only from Ecuador. The two species differ in numerous minor features, which, when combined with their separate ranges strongly suggest distinct entities. *Psammisia darienensis* possesses shorter pedicels (9–12 mm, not 12–20 mm), larger stamens (including longer filaments, anthers and tubules), pubescent filaments and connectives and a dehiscence cleft extending the length of the anther tubule. Also, the shape of the anther is different, the theca-tubule junction being straight in *P. darienensis*, and distinctly geniculate in *P. idalima*; the base of the theca is rounded and not incurved in the new species, while it is tapered and incurved in *P. idalima*. *Psammisia darienensis* also lacks the persistent bracts at the base of the inflorescence which are characteristic of *P. idalima*.

DARIÉN: Top of W ridge of Cerro Tacarcuna, elfin forest and transition between elfin forest and lower montane wet forest, 1800–1850 m, *Gentry & Mori 14024* (MO).

3. ***Psammisia dolichopoda*** A. C. Smith, Contr. U.S. Natl. Herb. 29: 368. 1950.
TYPE: Colombia; Cauca, *Haught 5199* (US, holotype; photo NY).

Epiphytic *shrub*, glabrous except for filaments, mature stems and twigs of the new growth terete or subterete, striate, reddish brown when dry. *Leaves* elliptic, subcoriaceous when dry, (5–)8–14 cm long, (2–)3–5 cm wide, basally cuneate or obtuse, short attenuate, apically long or short acuminate, weakly 5(–7)-plinerved, the midrib, the lateral nerves and the veinlets weakly raised above, more prominent beneath; petiole rugose, 4–5 mm long, 1–2 mm in diameter. *Inflorescence* racemose or subcorymbose, 5–8(–10)-flowered; rachis subterete or

angled, striate, 1.5–4 cm long, the peduncle 1–2 cm long; pedicels terete, striate, (20–)25–30 mm long at anthesis, lengthening to 40 mm post anthesis; floral bracts and the bracteoles minute, ovate, acute to acuminate, 0.5–1 mm long, fimbriate. *Flowers* with the hypanthium and calyx 5–5.2 mm long, obscurely articulate with the pedicel but without a clearly marked groove; the tube cylindric or slightly ribbed, ca. 3 mm long, 5 mm in diameter, the limb campanulate, 2.2–2.5 mm long including the calyx lobes, the lobes short-triangular, ca. 1.2 mm long, the sinuses broadly rounded or flat; corolla subglobose to urceolate, coriaceous, green when fresh, 5.5–6 mm long, 4–5 mm diameter, the lobes triangular, acute, ca. 1.2 mm long; stamens 4–5 mm long, without spurs but the connective broadly callose thickened, the filaments distinct, 1–2.5 mm long, 0.8–1 mm wide, attached to the upper part of the anther sac, ciliate or strigose along the dorsal surface, the anthers 3.5–4.5 mm long, the thecae coarsely granular, 2–3 mm long, tubules 1–1.5 mm long, dehiscing by elongate pores 0.5–0.7 mm long; style inserted, 4 mm long. Mature *berry* not seen.

The extension of the range of *P. dolichopoda* from the type locality in wet montane forest (2,500 m) to the tropical moist forest of the El Llano-Cartí area is surprising. The Panamanian material differs from that of the type collection in seemingly insignificant characters, e.g. rachis 6–8 cm long and corolla 7–9 mm long in the type collection vs. rachis 1.5–4 cm long and corolla 5.5–6 mm long in the Panamanian material.

PANAMÁ: El Llano-Cartí Road, 7–12 km from Interamerican Highway, 360–410 m, *Croat* 25160 (DUKE, MO), 26062, 26076; *D'Arcy* 10606; (all MO). *Dressler* 4674 (DUKE); *Gentry* 5798 (DUKE, MO); *Mori* 7752 (DUKE, MO); *Mori* & *Kallunki* 2301, 2903, 4714 (all MO). DARIÉN: Ascent of Cerro Pirre from Río Pirre S of El Real, 750–1030 m, *Duke* 5323 (MO). Cloud forest and mossy forest, Cerro Pirre, 2500–4500 ft, *Duke* & *Elias* 13764 (DUKE, MO).

4. ***Psammisia panamensis*** A. C. Smith, Ann. Missouri Bot. Gard. 28: 440. 1941.
TYPE: Panama: *Allen* 2152 (A, holotype).

Epiphytic *shrub* 0.5–1.0 m high, glabrous throughout except for the filaments; branchlets thick, terete. *Leaves* coriaceous when dry, oblong lanceolate to narrowly elliptic, 26–37 cm long, (3.5–)5.5–9.3 cm wide, basally cuneate, apically acute to gradually acuminate, entire and narrowly revolute, pinnately nerved, the midvein and the principal veins moderately elevated above, prominently so beneath, the veinlets reticulate and conspicuous; petioles rugose, 8–12 mm long, 3–4 mm in diameter. *Inflorescences* axillary, shortly racemose or corymbose at anthesis, 6–10-flowered with practically no peduncle; rachis 6–10 mm long, angled; pedicels 8–12 mm long, 1–1.5 mm in diameter, each subtended by a papery, ovate to deltoid, acute, usually minutely toothed bract 1.5–3 mm long and with 2 submedial, often toothed bracteoles 1.5–2 mm long. *Flowers* with the hypanthium and the calyx broadly campanulate at anthesis, 7–8 mm long, 5–7 mm in diameter at its summit, clearly disarticulating from the pedicel by a sharply delineated groove, the calyx limb slightly coriaceous, suberect, ca. 3 mm long including the lobes, the calyx lobes deltoid, acute, 2–2.5 mm long, basally 2–3 mm wide; corolla glabrous, somewhat fleshy, truncately conic at

anthesis, 6–10 mm long, at the base 5–8 mm in diameter, contracted apically, the lobes 5, deltoid, acute, 1–1.2 mm long and wide; stamens 10, the filaments submembranaceous, distinct, ligulate, 1.5–2 mm long, puberulent ciliate, apically tapering, the connectives either alternately obscurely 2-spurred and spurless or all spurless, the anther sacs rigid, 3.5–4 mm long, the base conspicuously incurved each with 2 cylindric-conical, connate tubules 1.5–2 mm long which dehisce introrsely by elongate oval clefts about as long as the tubules; stigma ca. 0.5 mm in diameter when receptive. Mature *berry* not seen.

This species is known only from the wet montane forests of central and eastern Panama.

COCLE: Hills N of El Valle de Antón, 1000 m, *Allen 2152* (A). DARIÉN: Cloud forest and mossy forest, Cuasí-Caña trail between Cerro Campamiento and La Escalera to "Paramo" E of Tres Bocas, *Kirkbride & Duke 1273* (MO). Lower montane rainforest, N slopes of Cerro Pirre, 700–950 m, *Mori & Kallunki 5477* (DUKE, MO). PANAMÁ: Cerro Jefe, *Croat 14441* (MO). Primary forest, Campo Tres, 3 km NE of Altos de Pacora, 500–800 m, *Croat 22752* (MO). Cerro Jefe, 4.6 km beyond peak on road to Altos de Pacora, 600 m, *Croat 35908* (MO). Altos de Pacora, 20–24 km NE of Cerro Azul, *Dressler 4612* (DUKE, MO). Cerro Jefe, near Río Indio, 2100–2200 ft, *Duke 15211* (MO). Secondary cloud forest, summit of Cerro Jefe, *Dwyer et al. 5045* (MO). Road beyond Cerro Jefe, *Foster 1486* (DUKE). Top of Cerro Jefe, *Gentry 4871* (DUKE, MO). Cloud forest, Altos de Pacora, 680–710 m, *Kennedy & Dressler 3512* (F). Premontane rainforest, 5–10 km NE of Altos de Pacora, 750 m, *Mori & Kallunki 4966* (MO). Caña, 5000 ft, *Williams 966* (NY). VERAGUAS: Primary forest on Caribbean slope above Río Primero Brazo 5 mi NW of Santa Fé, 700–1200 m, *Croat 23138* (DUKE, MO). 2.6 km from Escuela Agrícola Alto de Piedra, NW of Santa Fé, *Mori & Kallunki 4741* (MO). Lower montane wet forest 6–7 km W of Santa Fé on new road past agriculture school, *Nee 9874* (MO).

5. ***Psammisia ramiflora*** Klotzsch, *Linnaea* 24: 44. 1851. TYPE: "in locis alpestribus Veraguae Americanae centralis," *Warscewicz* (B, holotype, not seen; photo F, GH, NY).—FIG. 14.

P. symphystemona Donnell Smith, *Bot. Gaz. (Crawfordsville)* 20: 291. 1895. TYPE: Costa Rica: Prov. de Alajuela: Mariposa, 5500 ft, *Cooper 5842* (US, holotype; GH, US, isotypes; photo, NY).

Usually epiphytic *shrubs* with slender, terete, glabrous branchlets. *Leaves* oblong or ovate oblong, 8–19(–27) cm long, 3–7(–11) cm wide, basally cuneate to rounded, apically caudate acuminate, the tip often 2–4 cm long, entire, glabrous both above and below, 5-plinerved with the secondary nerves originating slightly above the base and ascending near the margins, the midvein slightly impressed or flush above and prominently elevated beneath, the veinlets conspicuously reticulate and elevated on both the surfaces but especially so beneath; petioles rugose, (3–)5–12(–17) mm long, glabrous, narrowly winged above. Inflorescence axillary, subfasciculate or short racemose, 4–15-flowered, the rachis less than 1 cm long, in fruit 1–4 cm long, glabrate throughout; pedicels slender, striate, 8–25 mm long, each subtended by an oblong or triangularly deltoid, persistent bract (1–)3–4 mm long and with 2, usually supramedial, deltoid, persistent bracteoles 1.5–2.5 mm long. *Flowers* with the hypanthium subcylindric or broadly obconic, ca. 3 mm long, 2.5 mm in diameter at the summit, glabrous, the calyx limb 3.5–4.5 mm long including the lobes, the lobes 5, triangular, acute, ca. 1.5 mm long; corolla subcylindric, red with a white tip, 20–35 mm long, 6–10



FIGURE 14. *Psammisia ramiflora* Klotzsch.—A. Habit ($\times \frac{2}{5}$).—B. Inflorescences ($\times \frac{2}{5}$).—C–D. Stamens.—C. Lateral view ($\times 3$).—D. Ventral view ($\times 3$). [After Utley & Utley 4453 (DUKE), Costa Rica.]

mm in diameter medially and near the base, contracted above to 4–5 mm in diameter before the elongate throat, the throat often with appressed glandular trichomes 0.1–0.4 mm long, the corolla lobes oblong, 2.5–3.5 mm long; stamens 10 (or in the rare 6-parted flowers, 12) 8–10 mm long, the filaments membranous, brown, 3.5–4.5 mm long, connate for their entire length or sometimes lightly coherent near the base or completely separate and leading into the connectives, the connectives narrow, ciliate with trichomes ca. 0.2 mm long, distally and alternately unequally 2-spurred, the anther sacs 3–3.2 mm long opening into pairs of tubules, the tubules, cylindric conic, 2–3 mm long, weakly coherent or

distinct to the base, opening introrsely by oval clefts about $\frac{3}{4}$ as long as the tubules; stigma truncate, the style exserted, 32–37 mm long, glabrous. *Berry* subglobose, 8–10 mm high, 10–13 mm in diameter.

This species, known only from Costa Rica and Panama, exhibits more variation than one would expect even in as variable a group as the thibaudioid ericads. The Chiriquí specimens all closely match the numerous Costa Rican representatives which mainly occur about the Meseta Central and especially in the Cordillera Central. Those specimens from the vicinity of Santa Fé in Veraguas have filaments ranging from weakly coherent to completely separate and their leaves seem more coriaceous with a slightly different venation pattern from the populations from Costa Rica and Chiriquí. The specimens seen from Coclé all have separate filaments. Specimens from Panamá and Darién all seemingly have connate filaments but with leaves slightly different from those from Costa Rica and Chiriquí both in texture and venation.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1500–2000 m, *Allen* 1503 (GH, MO, NY, US). Cloud forest 1–2 km N of Las Nubes and W of Cerro Punta peak, 5 km NW of Cerro Punta, 2000–2200 m, *Almeda* 1536 (DUKE). Rich cloud forests, Las Nubes, 5.5 km NW of Río Chiriquí Viejo, 2200 m, *Busey* 665, *Croat* 26447 (both MO). Cerro Colorado Copper Mine Development, 28 mi above San Félix, 9–10 mi above turnoff to Escopeta, 1200–1500 m, *Croat* 33197 (MO). Wet river gorge, Río Chiriquí Viejo above town of Cerro Punta, 6000–8000 ft, *D'Arcy* 6580 (MO). Bajo Chorro, Boquete, *Davidson* 59 (A, F, MO, US). Rain forest, Bajo Chorro, 6000 ft, *Davidson* 606, 607 (both F). Slopes of Cerro Punta, 2000 m, *Gentry* 5865 (DUKE, F, MO, NY). Rain forest, Cerro Horqueta, 6500 ft, *Hagen* 2026 (A, NY). Premontane forest between Pinola and Quebrada Hondo on Chiriquí Trail towards summit, *Kirkbride & Duke* 897 (MO, NY). Cloud forest below Divide on Chiriquí Trail, *Kirkbride & Duke* 965 (MO, NY). Las Nubes, 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Liesner* 298 (DUKE, MO). Above Las Nubes, NW of Cerro Punta, 1900–2100 m, *Luteyn* 3803 (DUKE); *Mori & Bolten* 7252 (DUKE, MO). Finca Collins, Boquete, 5800–6700 ft, *Stern, Eyde & Ayensu* 2025 (MO, US). Between Bajo Quiel and Bajo Mono 6 mi NW of Boquete, 1450 m, *Wilbur et al.* 12016 (DUKE). Mossy forest, 7000 ft, E of Guadeloupe along the Río Chiriquí Viejo 2 mi NE of Cerro Punta, *Wilbur & Teeri* 13100B (DUKE, MO). Wet mossy forest 7500 ft on NW side of Cerro Punta beyond Las Nubes, *Wilbur & Teeri* 13221 (DUKE, F, LL, MICH, MO, PMA). COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen* 2192 (A, MO), 2337 (MO). Trail to Cerro Pilón WEPCOR weather station, 1 km from top, 900 m, *Correa* 47 (FSU, SCZ). Cloud forest at La Mesa above El Valle, *Croat* 13409 (MO). La Mesa above El Valle, 800 m, *Croat* 25347 (DUKE, MO). Road past Furlong's Finca due N of Cerro Pilón, 880 m, *Croat* 37551 (MO). Cloud forest on slopes of Cerro Pilón near El Valle, 700–900 m, *Duke* 12130 (MO). Cloud forest, El Valle, 800–1000 m, *Duke* 13204 (MO). Foothills of Cerro Pilón near El Valle, *Duke & Correa* 14691 (MO). Between Cerro Pilón and El Valle, 700–900 m, *Duke & Dwyer* 13948 (DUKE, MO). El Valle, *Dwyer* 1936 (MO). Cerro Pilón, *Dwyer* 8354 (MO, NY). 8.5 mi from El Valle toward La Mesa, *Dwyer* 10535 (MO). El Valle de Antón at the foot of Cerro Pilón, ca. 2000 ft, *Dwyer & Correa* 8008 (DUKE, MO, SCZ). Cerro Gaítal, Caracoral, 2700 ft, *Dwyer & Correa* 8911 (MO). Cerro Pilón, 2700 ft, *Dwyer & Lallathin* 8649 (MO). Summit of Cerro Pilón above El Valle de Antón, 2700 ft, *Dwyer et al.* 4514 (MO). 2.5 mi W of El Valle, *Gentry & Dwyer* 3614 (DUKE, F). La Mesa above El Valle, 1000 m, *Gentry* 5654 (MO). La Mesa, N of El Valle, 1000 m, *Gentry* 6824 (DUKE, MO). Cloud forest, La Mesa, 800 m, *Kennedy et al.* 2089 (DUKE, MO). Cerro Caracoral, elfin forest, *Kirkbride* 1103 (MO). Cloud forest 6 mi N of El Valle de Antón, 1000 m, *Luteyn* 1158 (DUKE). La Mesa, 2.8–3.4 mi NW of El Valle de Antón, 850–900 m, *Luteyn* 4071 (DUKE). Road 8 mi N of El Valle de Antón, *Luteyn & Kennedy* 1725 (DUKE). La Mesa 4 km N of El Valle, 875 m, *Nee & Dwyer* 9140, *Nee & Dwyer* 9148, *Nee & Dwyer* 9625 (all MO). Cloud forest, along road from El Valle to La Mesa, 2400–2600 ft, *Spellman et al.* 584 (DUKE, MO). Near El Valle de Antón, *Stockwell* (DUKE). Above El Valle on road to La Mesa, 2500 ft, *Tyson* 6935 (PMA). El Valle de Antón, near La Mesa, 5 mi N of El Valle, *Wilbur & Luteyn* 11747 (DUKE). 1000 m on La Mesa below the N rim, *Wilbur et al.* 11153

(DUKE, F, MO, NY, PMA, US). La Mesa 3 km N of El Valle de Antón, 850 m, *Wilbur et al.* 15651 (DUKE, MO). N rim of El Valle de Antón near Cerro Turega, 650–700 m, *Woodson & Schery* 184 (MO, NY). COLÓN: Trail at end of Santa Rita Ridge Road, 600–800 m, *Mori & Crosby* 6432 (MO). DARIÉN: Cerro Pirre, *Bristan* 614 (MO). Trail from Pucuro to Cerro Mali, near La Laguna, ridge between Pucuro and Tapalisa Rivers, 820–840 m, *Gentry & Mori* 13553 (MO). Cloud forest and mossy forest, Cuasi-Caña Trail between Cerro Campamiento and La Escalera to "Paramo," E of Tres Bocas, *Kirkbride & Duke* 1327 (MO, NY). N slopes of Cerro Pirre, 700–950 m, *Mori & Kallunki* 5475 (MO). PANAMÁ: Después de La Eneida, 750 m, *Correa et al.* 805 (DUKE, F, MO, PMA). Camino de Llano a Cartí, 400 m, *Correa et al.* 1889 (DUKE, MO, PMA). 6 mi above Goofy Lake on road to Cerro Jefe, *Croat* 15217 (MO). Primary forest along newly cut road from El Llano to Cartí-Tupile 12 mi above Panamerican Highway, 200–500 m, *Croat* 22855 (MO), 22865 (DUKE, MO). Summit of Cerro Jefe, *Dwyer et al.* 5026 (DUKE). Cerro Azul, 3000 ft, *Goldman* 1870 (US). 14–17.5 km on road from El Llano to Cartí-Tupile, 200–500 m, *Kennedy* 2498 (F, MO, NY). Lowland cloud forest, between Cerro Azul and Cerro Jefe, 1000 m, *Luteyn* 3202 (DUKE, NY), 3210 (DUKE). Top of Cerro Jefe, 3000 ft, *Luteyn & Kennedy* 3970 (DUKE). El Llano-Cartí Road, 18.8 km from Interamerican Highway, 350 m, *Mori & Kallunki* 5133 (DUKE, MO). Ridge running NE of summit of Cerro Jefe, 1000 m, *Mori & Kallunki* 6096 (DUKE). El Llano-Cartí Road, 12.7 km from Interamerican Highway, 350 m, *Mori et al.* 4684 (MO). Top of Cerro Jefe, 3140 ft, *Tyson* 3587 (FSU, MO, SCZ). Cerro Jefe, *Witherspoon* 8549 (MO). VERAGUAS: Forested slopes of Cerro Tute, near Santa Fé, 3000 ft, *Allen* 4353 (MO, US). 5 mi W of Santa Fé on road past Escuela Agrícola Alto Piedra on Pacific side of divide, 800–1200 m, *Liesner* 881 (DUKE, MO). Santa Fé, subiendo Cerro Tute, *Mendieta* 573 (PMA). 8.8 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki* 3230 (DUKE, MO). Forest 6–7 km W of Santa Fé on new road past agriculture school, 2900 ft, *Nee* 9794 (DUKE, MO).

15. SATYRIA

Satyria Klotzsch, *Linnaea* 24: 14, 21. 1851. LECTOTYPE: *Satyria warszewiczii* Klotzsch.

Epiphytic or terrestrial *shrubs*. *Leaves* alternate, coriaceous, usually plinnerved but rarely pinnately veined, petiolate. *Inflorescence* terminal or axillary, often cauliflorous, racemose or subfasciculate with few to many, often pendent flowers; pedicels minutely bibracteolate, each subtended by a small bract. *Flowers* with the hypanthium subglobose to shortly campanulate, a sharply delineated disarticulation groove at its juncture with the pedicel, the calyx limb flaring or spreading, the lobes (3–4)5, ovate to triangular or merely apiculate; corolla cylindric to narrowly vasiform, the lobes 5, triangular to narrowly oblong, acute; stamens 10 of alternately unequal lengths, shorter than the corolla and usually only about $\frac{1}{3}$ as long, the filaments equal and firmly connate into a monadelphous tube for more than half their length, membranous to thinly coriaceous, the anthers dorsally attached near their bases, the anther sacs subcoriaceous, firm, alternately unequal in length and dimorphic with slightly granular thecae, the flaring tubules not sharply differentiated from the anther sacs, opening by oblique clefts; stigma usually truncate, the style filiform and as long as the corolla or slightly exserted, the ovary inferior.

Satyria is a well-marked, largely montane genus of approximately twenty five species ranging from southern Mexico to Bolivia and east to French Guiana.

- a. Hypanthium and corolla densely puberulous; filaments glabrous; corolla 10–13(–16) mm long 1. *S. allenii*
- aa. Hypanthium and corolla glabrous; filaments ciliate; corolla (15–)17–28 mm long 2. *S. warszewiczii*

1. *Satyria allenii* A. C. Smith, Ann. Missouri Bot. Gard. 28: 451. 1941. TYPE: Panama: Allen 2367 (A, holotype).

Epiphytic, much branched *shrub* or woody *vine* with branches to 2.5 m long; branchlets thick, subterete, angled when young, somewhat cinereous. *Leaves* coriaceous, glabrous, elliptic oblong (4-)6-10(-16.5) cm long, (2-)3-6(-10) cm wide, basally acute, cuneate or rounded, apically cuspidate, the obtuse acumen to 4 mm long, entire, the margin often conspicuously recurved, 5-plinerved, the interior veins often originating 1-2 cm above the base, with the midvein impressed above and prominently elevated beneath; petioles rugose, glabrous, thickened, 6-10 mm long. *Inflorescences* borne on leafless branches, shortly racemose, 2-6 flowered, the rachis slender, glabrous, 6-10 mm long; pedicels "coral pink," slender, distally slightly swollen, whitish puberulent, (6-)9-12 mm long, the bract oblong ca. 1.5 mm long, usually submedial but occasionally medial or supramedial, the bracteoles 2, inconspicuous, narrowly triangular, appressed, 1.5-2 mm long. *Flowers* with the hypanthium "coral pink," 1-2 mm long and 1-2 (-3) mm in diameter, externally densely spreading puberulent with whitish, persistent trichomes 0.2 mm long; calyx limb spreading erect, ca. 2 mm long, slightly fleshy, the lobes 5, deltoid, acute, ca. 1 mm long, 2.5 mm wide; corolla "coral pink" but distally pure white, densely spreading puberulous throughout, fleshy, cylindric, 10-13(16) mm long, 2-3 mm in diameter basally and at the throat, the lobes 5, acute, ca. 0.7 mm long, 1.3 mm wide; stamens 10, alternately 4 mm long and 4.5 mm long, the filaments glabrous, united in a pale, membranaceous tube 2.5-4 mm long, the anthers alternately 2-3 mm long and 2.3-3.8 mm long, the tubules opening by broad clefts ca. 0.6 mm long; stigma minute, subpeltate, the style slender, 1-2 mm longer than the corolla or equalling it. *Berry* (4-)5-7 (8) mm in diameter, 3-4 mm high, capped by the inflexed, acutely deltoid calyx lobes and with a markedly swollen basal enlargement 3-5 mm in diameter just beneath the disarticulation groove.

COCLÉ: Hills N of El Valle, 1000 m, Allen 2335 (A), 2336 (MO). La Mesa N of El Valle de Antón, 1000 m, Allen 2367 (A). El Valle de Antón, 1000 m, Allen 3415 (F, GH, US). Trail beyond La Mesa towards Los Llano, 800-860 m, Luteyn 3167 (DUKE). La Mesa below the N rim on forested slopes, Wilbur 11152 (CAS, DUKE, F, GH, LL, MICH, MO, NY, PMA, US, WIS). PANAMÁ: Cerro Jefe, Busey & Croat 275 (DUKE, MO); Correa 716 (MO); Croat 13029 (DUKE, MO); Croat 13080 (DUKE, MO); Duke 8174 (MO), 9397 (MO, US), 9426 (MO); Dwyer et al. 5026 (DUKE, MO); Dwyer et al. 7275 (MO); Dwyer 8256 (MO); Gentry & Dwyer 3423, 3496 (both DUKE, MO); Gentry & Mori 13435 (DUKE, MO); Liesner 583 (DUKE, MO). Cerro Campana, 850 m, Liesner 599 (DUKE, MO). Cerro Jefe, 1000 m, Luteyn & Wilbur 4656 (DUKE); Maas & Dressler 697 (MO). Cloud forest, Cerro Campana, ca. 10 km SW of Capira, Mori & Kallunki 3582 (DUKE, MO). Cerro Campana, rainforest above Su Lin Motel, Porter et al. 4208 (MO). E slope of Cerro Jefe, 2700 ft, Tyson 3380 (GH, MO, SCZ); Tyson 3530 (MO, SCZ). Cerro Campana, 2500 ft, Tyson 5327 (FSU, MO, SCZ). Slopes of Cerro Jefe beyond Cerro Azul 5.5 m on road to La Eneida, Wilbur & Teeri 13644 (CAS, CR, DUKE, F, GH, LL, MICH, MO, NY, PMA, UC, US, WIS). Wind-swept mossy crest, slopes of Cerro Campana, 2700 ft, Wilbur & Weaver 11294 (DUKE). Slopes of Cerro Jefe beyond Cerro Azul, Wilbur & Weaver 11376 (DUKE).

2. *Satyria warszewiczii* Klotzsch, Linnaea 24: 22. 1851. TYPE: Panama (?), "in Veragua," Warszewicz (B, holotype, not seen).—FIG. 15.

S. clonantha Klotzsch, Linnaea 24: 22. 1851. TYPE: Panama (?), "in Veragua," Warszewicz s.n. (B, holotype, not seen).

Riedelia warszewiczii (Klotzsch) Kuntze, Rev. Gen. Pl. 2: 384. 1891.

R. clonantha (Klotzsch) Kuntze, Rev. Gen. Pl. 2: 384. 1891.

Epiphytic or terrestrial straggly *shrub*; branches 1–2.5(4) m long, stout, terete, glabrous, grayish to brown or reddish brown. *Leaves* oblong, ovate oblong, lance oblong or elliptic, (6–)10–25(–29) cm long, (2–)4–10(–14) cm wide, basally cuneate, rarely rounded, apically acute to acuminate, entire, slightly revolute, chartaceous to coriaceous, glabrous or rarely inconspicuously glandular strigillose beneath, trichomes 0.2 mm long or less, drying reddish brown; 3–(5)-plinerved, the midvein and the principal paralleling veins either impressed or slightly elevated on the upper surface and prominently elevated beneath, the veinlets drying reticulate slightly elevated on both the surfaces. *Inflorescences* often numerous, pendent, usually cauliflorous, either arising from a low padlike mound or shortly racemose, 3–10(–30)-flowered; rachis striate, glabrous, 5–15(–40) mm long; glabrous or rarely sparsely puberulent, terete, often distally swollen, 8–20(–25) mm long; bract basal, inconspicuously ciliate, triangular, (1.8–)2–3(–4) mm long, bracteoles 2, alternate, narrowly triangular, acute, inconspicuously ciliate, 1–1.5(–2) mm long. *Flowers* with the hypanthium glabrous, coriaceous, campanulate, occasionally slightly enlarged at the base. 1.5–2.5 mm high, 3–4.2 mm in diameter at anthesis, the calyx limb drying thinly coriaceous, nearly truncate, slightly flaring, 1.5–2.2(–3.0) mm long including the lobes, the lobes minute, apiculate; corolla usually carnose but often drying as though thinly textured, cylindric or tapering to the slightly flaring throat, occasionally thin waisted with a somewhat swollen base and distally flaring, (15–)17–28 mm long, mostly (2–)3–5 mm in diameter, usually bright red for the basal $\frac{3}{4}$ and apically white, the lobes acute, oblong, 1–2 mm long; stamens 10, staminal tube 1.5–2(–3.0) mm long glabrous the free portion of the anthers ciliate, the thecae alternately 3.8–5 mm long and 4.8–6 mm long, dehiscing by oval clefts 1.8–2.5 mm long; style 18–30 mm long and usually exerted 2–3 mm beyond the corolla, long persisting. *Berry* often glaucous, 5–6 mm high, 7–8 mm in diameter.

This wide-ranging species is known from southern Mexico south to at least eastern Panama. There is considerable morphological variability in the shape and venation of the leaves and in the size of the flowers. The extremes are strikingly unlike but efforts to subdivide the species have met with failure.

BOCAS DEL TORO: Elfin forest on Chiriquí Trail, E slope of La Zorra to Divide, *Kirkbride & Duke* 808 (MO, NY). CHIRIQUÍ: Llanos on slopes of Volcán de Chiriquí Viejo and along Río Chiriquí Viejo, 1200 m, *Allen* 976 (F, MO). "New Switzerland," central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen* 1388 (GH, NY, US). Cerro Punta, 2000 m, *Allen* 3494 (F, GH, MO, US). Between Bambito and Cerro Punta, *Croat* 10636 (DUKE, MO). Forested hill N of Audubon Cabin, *Croat* 13658 (DUKE, MO). Above San Félix along mining road 18–27 mi from Panamerican Highway, 1200–1500 m, *Croat* 33051 (NY). Cerro Colorado Copper Mine development, 28 mi above San Félix, 1200–1500 m, *Croat* 33248 (MO). Above Cerro Punta on slope of Cerro Respinga, Bajo Grande, 8000 ft, *D'Arcy* 6558 (DUKE, MO). Bajo Chorro, Boquete District, 6000 ft, *Davidson* 60 (MO), 80 (F), 608 (MO, US). Boquete, 3800 ft, *Davidson* 653 (F, MO). Between Boquete and Cerro Horqueta, *Duke* 13722 (DUKE, SCZ). 1.4 km S of Cerro Punta, 1850 m, *Graham* 289 (GH). Cerro Punta 2.5 km S of Audubon Cabin, 6000 ft, *Kozlovsky* K-11, K-16 (both MO, WIS). Cloud forest, Cerro Horqueta, 5800 ft, *Lewis et al.* 538 (MO). Las Nubes, 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Liesner* 303 (DUKE, MO). Cerro Punta, *Lindsay* 469 (F,



FIGURE 15. *Satyria warszewiczii* Klotzsch. Habit ($\times \frac{1}{2}$). [After Wilbur & Luteyn 19173 (DUKE).]

MO). Bajo Chorro Trail towards Boquete from Cerro Punta, 7000 ft, *Luteyn* 3058 (DUKE). Bajo Mono Trail NW of San Ramón towards headwaters of Río Caldera, 1600–1700 m, *Luteyn* 3726 (DUKE). Heavily forested slopes along ridge on W side of Cerro Horqueta, 1700–1800 m, *Luteyn* 3761 (DUKE, MO). Las Nubes, 5 km NW of Cerro Punta, 6000–6500 ft, *Mori & Bolten* 7251 (MO). Cerro Colorado Copper Mine Rd along continental divide N of San Félix, *Mori & Kallunki* 5804 (DUKE, MO), 5904, 5938 (both MO). Bajo Grande, 1–3 km E of town of Cerro Punta, *Nee* 10055 (MO). Forests around Boquete, 1000–1300 m, *Pittier* 3014 (US). N facing cliff just S of Boquete, *Stern et al.* 1958 (MO, US). Mossy forest E of Guadeloupe 2 mi NE of Cerro Punta Ridge, *Wilbur & Foster* 13100 (DUKE, F, MO).

Beyond Las Nubes, *Wilbur & Teeri* 13223 (DUKE, MO). Slopes above Río Caldera 3 km beyond Bajo Mano, *Wilbur & Luteyn* 19173 (DUKE). Halfway between Cerro Punta and Bambito, *Wilbur et al.* 10948 (DUKE, F, GH, MO, NY, PMA). Steep forested slopes NE of Cerro Pando NW of Nueva California, 1500 m, *Wilbur et al.* 11016 (DUKE, MO). COCLÉ: Cerro Pilón above El Valle de Antón, 2000–2700 ft, *Dwyer* 4568 (DUKE, MO). Cloud forest 3 km NE of El Valle, *Mori & Kallunki* 2963 (DUKE, MO). La Mesa, *Nee & Dwyer* 9158 (MO). La Mesa 5 mi N of El Valle, 2500 ft, *Tyson et al.* 2449 (FSU, SCZ). DARIÉN: Cerro Pirre, *Bristan* 538 (DUKE, MO, SCZ). Elfin forest, Cerro Campamento S of Cerro Pirre, *Duke* 15673 (MO). Cerro Pirre, 2500–4500 ft, *Duke & Elias* 13722 (DUKE, MO). Summit of Cerro Pirre, cloud forest, *Gentry & Clewell* 6965 (DUKE, MO). Top of Cerro Mali, *Gentry & Mori* 13657 (DUKE, MO). Elfin forest, top of W peak of Cerro Tacarcuna massif, 1800–1850 m, *Gentry & Mori* 13978 (DUKE, MO). PANAMÁ: Cerro Campana, 800 m, *Allen* 2082 (NY), 3962 (NY, US). Rainforest 15.5 km N of El Llano on road to Cartí, 400 m, *Busey* 364 (DUKE, MO). El Llano to Cartí-Tupile road 12 mi above Panamerican Highway, 200–500 m, *Croat* 22900 (DUKE, MO). El Llano-Cartí road, 5–6 mi N of Interamerican Highway, 350–375 m, *Croat* 34775 (NY). Cerro Campana, *Dressler* 4518 (DUKE, F, MO, PMA). Cerro Jefe, 3600 ft, *Duke* 8174 (DUKE). Cerro Campana, 800–1000 m, *Gentry* 4950 (MO). Forest 4.8 mi N of Panamerican Highway just W of El Llano, *Gentry* 5084 (DUKE, MO). Near summit of Cerro Jefe, *Gentry & Dwyer* 5525 (MO). Cerro Jefe, cloud forest, 800–1000 m, *Gentry & Mori* 13448 (DUKE, MO). 16 km above Panamerican Highway on road from El Llano to Cartí-Tupile, *Kennedy et al.* 2440 (MO). Tropical wet forest, 10–12 km N of Interamerican Highway along El Llano-Cartí-Tupile road, *Luteyn & Wilbur* 4670 (DUKE); *Mori & Kallunki* 2310, 2878, 2923 (all DUKE, MO). Premontane rainforest NE of Cerro Azul, *Mori & Kallunki* 3642 (MO). El Llano-Cartí road 20.9 km from Interamerican Highway, *Mori & Kallunki* 5583 (MO). El Llano-Cartí road 11–12 km from Interamerican Highway, 300–400 m, *Mori et al.* 6878 (MO). El Llano-Cartí road 8–12 mi N of El Llano, 400–450 m, *Nee et al.* 8751 (DUKE, MO). Cerro Jefe, 2700–3000 ft, *Tyson et al.* 3293 (MO). VERAGUAS: Forested slopes of Cerro Tute, vicinity of Santa Fé, 3000 ft, *Allen* 4354 (MO, US). Primary forest on Caribbean slope above Río Primero Brazo, 5 mi NW of Santa Fé, 700–1200 m, *Croat* 23121 (MO). 5 mi W of Santa Fé on Pacific side of divide, 800–1200 m, *Croat* 23154 (MO), 23155 (DUKE, MO). 3.9–5 mi N of Santa Fé, 500–1000 m, *Gentry* 2993 (MO). 5 mi W of Santa Fé on Pacific side of divide, 800–1200 m, *Liesner* 938 (MO). Above Santa Fé in Pacific watershed, *Luteyn & Wilbur* 4555 (DUKE). On slopes of Cerro Tute NW of Santa Fé, *Mori & Kallunki* 4776 (DUKE, MO). 7 km W of Santa Fé, ca. 2900 ft, *Nee* 11200 (MO). Forest 3–4 km W of Santa Fé, ca. 2500 ft, *Nee* 11270 (DUKE, MO).

16. SPHYROSPERMUM

Sphyrospermum Poepp. & Endlich., Nov. Gen. Sp. Pl. 1: 4. 1835. LECTOTYPE: *S. buxifolium* Poeppig & Endlicher.

Sophoclesia Klotzsch, Linnaea 24: 15, 29. 1851.

Slender, often straggly, epiphytic or terrestrial *shrubs* frequently with pendent branches. *Leaves* usually small and obscurely nerved, coriaceous, subsessile. *Inflorescences* usually few, solitary or rarely paired flowers in the axils of the leaves; pedicels slender, cernuous, distally swollen; bracteoles 2, deciduous. *Flowers* with the hypanthia continuous with the pedicel, subglobose or obconic, the calyx limb suberect, the lobes 4–5; corolla cylindric to campanulate, 4–5-lobed; stamens usually as many or twice as many as the corolla lobes, equal or alternately slightly unequal, the filaments slender, ligulate, the anthers inserted dorsally near the base, membranous, smooth, usually shorter than the filament, the 2 distinct tubules as long as or longer than the locules, opening by oval, introrse clefts; stigma truncate, the style filiform, about as long as the corolla. *Fruit* a subglobose or ellipsoid, berry with a smooth or pubescent, brittle pericarp, dry but becoming succulent at maturity, topped by the persistent

calyx limb and lobes, 4–5 loculed, the partitions soon decaying; ovules numerous, axile but often appearing central or even basal; seeds elongate, striate, the green embryo visible through the endosperm.

Sphyrospermum is a troublesome genus of perhaps 20 species. It ranges from southern Mexico and Haiti to Trinidad and French Guiana, through the highlands of Central America and the Andes of South America to Bolivia.

Literature:

Smith, A. C. 1933. The genera *Sphyrospermum* and *Disterigma*. *Brittonia* 1: 203–232.

- a. Hypanthia pilosulose, strigillose to glabrous or nearly so, the trichomes when present, always slenderly based.
 - b. Corolla 4 mm long or longer; hypanthium often moderately to densely pilosulose or puberulous as well as glandularly strigillose.
 - c. Leaves suborbicular to oblong ovate, (7–)9–15(–18) mm long; stamens 4
 ----- 1. *S. buxifolium*
 - cc. Leaves ovate to lance ovate, (15–)20–50 mm long; stamens 4–10, 7(–70)
 ----- 2. *S. cordifolium*
 - bb. Corolla less than 2.5 mm long; hypanthium minutely strigillose but never pilosulose or puberulous
 ----- 3. *S. standleyi*
 - aa. Hypanthia densely tuberculate, the modified trichomes with greatly swollen bases
 ----- 4. *S. tuberculatum*

1. ***Sphyrospermum buxifolium*** Poepp. & Endlich., *Nov. Gen. Sp. Pl.* 1: 4. *pl.* 8. 1835. TYPE: Peru, *Poeppig* (B, holotype; P, isotype; photos of both NY).

Sophoclesia nummulariaefolia Klotzsch, *Linnaea* 24: 30. 1851. TYPE: Colombia; *Moritz* 1339 (B, not seen; fragm. NY).

Sphyrospermum Roraimae Klotzsch, *Linnaea* 24: 36. 1851. TYPE: Guyana, *Schomburgk* 975 (B, not seen; fragm. & photo NY).

Sophoclesia cordifolia var. *oophylla* Kuntze, *Rev. Gen. Pl.* 2: 384. 1891. TYPE: Costa Rica, *Kuntze* 2153 (NY, holotype).

Vaccinium pachycardium Standley, *Fieldiana, Bot.* 18: 883. 1938. TYPE: Costa Rica, *Standley & Torres* 51769 (US, holotype).

Epiphytic or terrestrial *shrublets* mostly 1.5–4 dm tall; branches slender, pendent to ascendent, glabrate; branchlets brownish and minutely pale puberulous, glabrescent. *Leaves* coriaceous, suborbicular to oblong ovate, (7–)9–15(–18) mm long, 8–20 mm wide, basally subcordate or rounded, apically rounded or obtuse, marginally entire and slightly recurved, sparsely and inconspicuously pilosulose on both the surfaces but becoming glabrate, also usually inconspicuously glandular strigillose beneath, obscurely 3- to 5-nerved from the base, the veins flush with the surface or slightly raised, obscurely reticulate above; petioles ca. 1 mm long, puberulous to glabrate. Pedicels glabrous to sparingly pilose, slightly and gradually swollen distally, (5–)10–18 mm long. *Flowers* with the hypanthium pilose to glabrate, subglobose, 1–1.5 mm in diameter; calyx limb suberect, short, ca. 0.5 mm long including the lobes, the lobes 4, apiculate and separated by rounded sinuses with a tuft of pilosulose trichomes or glabrous; corolla white to pinkish, submembranous, 4–6 mm long, 1–1.5 mm in diameter, sparsely pilose to glabrous, the corolla lobes 4, narrowly triangular, minute, 0.8–1 mm long; stamens 4, equal, slightly shorter than the corolla, the

filaments either sparsely villose or glabrous, 1.8–3 mm long, the anthers smooth, 1.8–2.5 mm long, the tubules about as long as the thecae. *Berry* subglobose, pilose or glabrous, 4–6 mm in diameter, succulent and whitish with a violet or lavender tinge.

This species ranges from the mountains of Nicaragua south into Bolivia and east into the Guyanas. Distinguishing it from some small-leaved specimens of *S. cordifolium* that have usually been treated as *S. majus* is not easy. A. C. Smith (1933) suggested the possibility that "*S. majus* is a hybrid between *S. buxifolium* and *S. cordifolium*."

CHIRIQUÍ: Disturbed cloud forest at Monte Rey above Boquete, *Croat* 15723 (MO). Chiquero, Boquete District, 5500 ft, *Davidson* 532 (F, MO). Bajo Mono and Quebrado Chiquero, 1500 m, *Woodson* 575 (GH, NY). COCLÉ: El Valle, N rim, 800–1000 m, *Allen* 1830 (MO). Cerro Pilón near El Valle, 700–900 m, *Duke* 12051, 12081 (both MO). Between Cerro Pilón and El Valle de Antón, 700–900 m, *Duke & Dwyer* 13929, 13990 (both MO). El Valle, *Ebinger* 1112 (F, MO). La Mesa near Cerro Pilón, El Valle, *Hladik* 374 (MO). Trail to La Mesa 4.5 mi beyond El Valle de Antón, *Wilbur & Luteyn* 11671 (DUKE, F, MICH, MO, NY). DARIÉN: Headwaters of Río Tuquesa 2 km from continental divide, *Croat* 27236 (MO). Elfin forest, Cerro Pirre, 2500–4500 ft, *Duke & Elias* 13700 (MO). PANAMÁ: Cerro Campana, *Croat* 12152 (MO). El Llano-Cartí highway 19 km N of El Llano, *Dressler* s.n. (DUKE). N of Santa Fé 2 km N of Escuela Agrícola Alto de Piedra, *Mori & Kallunki* 2579 (MO). NW of Santa Fé, 8 km from Escuela Agrícola Alto de Piedra, Pacific slopes, *Mori & Kallunki* 3934 (MO). Tropical wet forest 16 km NW of Santa Fé on road to Calovebora, *Mori & Kallunki* 6143 (MO). Lower montane wet forest 6–7 km W of Santa Fé, 2900 ft, *Nee* 9855 (MO). Cut-over slopes 2 km N of Santa Fé towards the continental divide, *Wilbur & Luteyn* 19117 (DUKE). Forest near second branch of Río Santa Maria along road from Santa Fé, *Witherspoon & Dressler* 8890 (DUKE, MO).

2. ***Spherospermum cordifolium*** Benth., Pl. Hartw. 222. 1846. TYPE: Colombia, *Hartweg* 1215 (K, holotype, not seen; BREM, isotype, not seen; photo NY).—FIG. 16.

Sophoclesia cordifolia (Benth.) Klotzsch, Linnaea 24: 29. 1851.

S. subscandens Klotzsch, Linnaea 24: 30. 1851. TYPE: Venezuela, *Moritz* 1338 (B, holotype, not seen; fragm. & photo NY).

S. ovata Klotzsch, Linnaea 24: 30. 1851. TYPE: Venezuela, *Moritz* 1340 (B, holotype, not seen; fragm. NY).

S. flaccida Seemann, Bot. Voy. Herald 164. 1854. TYPE: Panama; Darién, *Seemann* (K, holotype, not seen; fragm. NY).

Spherospermum majus Griseb., Fl. Brit. W.I. 143. 1859.

Sophoclesia major (Griseb.) Benth. & Hook., Gen. Pl. 2: 576. 1876.

S. cordifolia var. *normalis* O. Kuntze, Rev. Gen. Pl. 2: 384. 1891. TYPE LOCALITY: Costa Rica.

S. robusta Rusby, Descr. S. Amer. Pl. 77. 1920. TYPE: Bolivia, *Bang* s.n. (NY, holotype).

S. trinitensis Britt., Bull. Torrey Bot. Club 48: 335. 1922. TYPE: Trinidad, *Britton et al.* 1316 (NY, holotype).

S. domingensis Urb. & Ekman, Ark. Bot. 21A(5): 54. 1927. TYPE: Haiti, *Ekman* 5219 (B, holotype, not seen; fragm. & photo NY).

Vaccinium valerii Standley, Fieldiana, Bot. 18: 884. 1938. TYPE: Costa Rica, *Standley & Valerio* 51853 (F, holotype).

Themistoclesia valerii (Standley) Sleumer, Bot. Jahrb. Syst. 71: 390. 1941.

Epiphytic or terrestrial *shrublets*, mostly 2–6 dm tall, the branchlets densely spreading puberulous, glabrescent. *Leaves* coriaceous, ovate, to lance ovate, (1.5–)2.0–5.0(–7.0) cm long, (10–)15–25(–32) cm wide, basally rounded or subcordate and apically obtuse or rounded to acute, marginally entire and

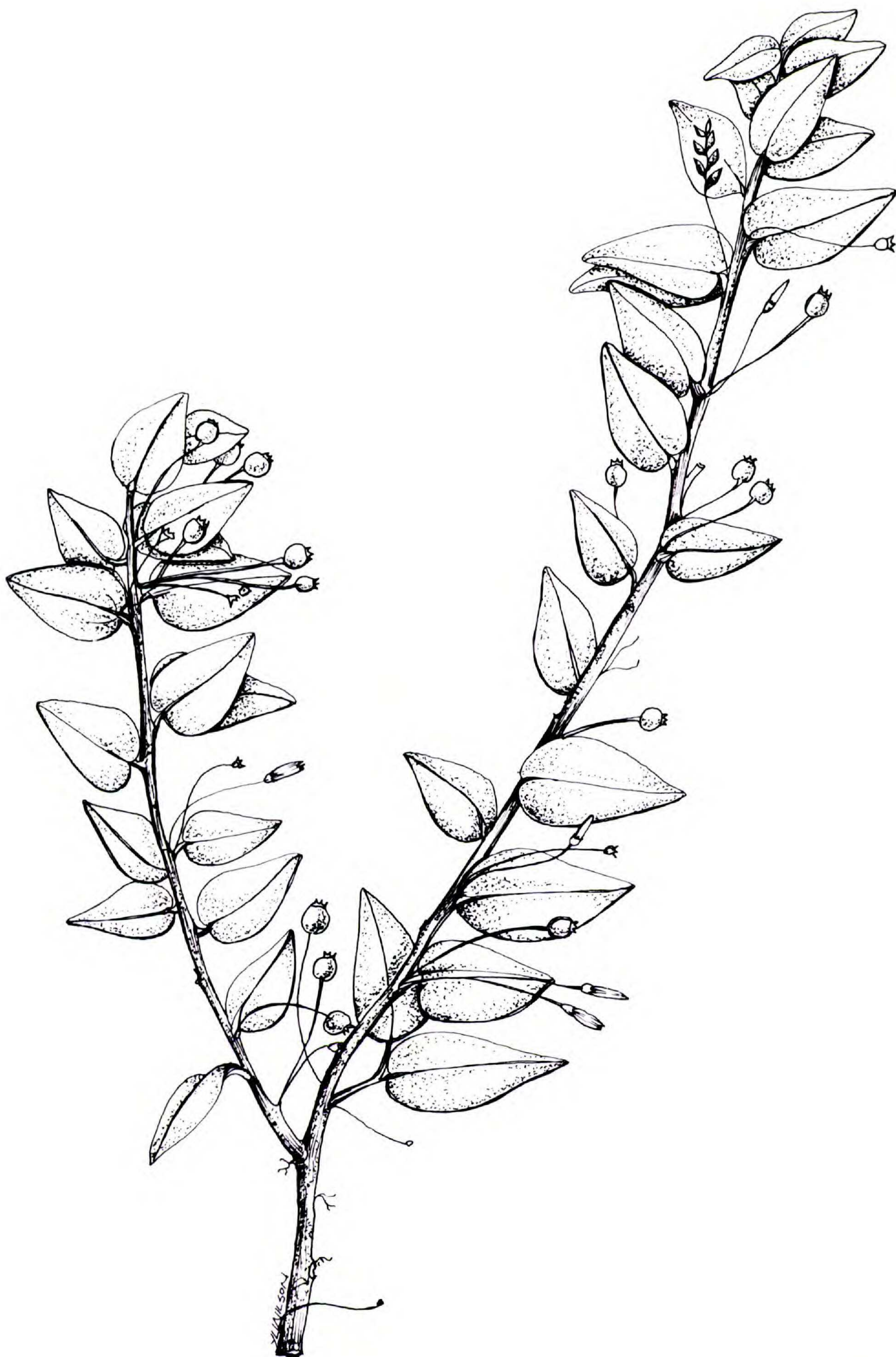


FIGURE 16. *Sphyrospermum cordifolium* Benth. Habit ($\times 1$). [After Wilbur & Luteyn 19402 (DUKE).]

slightly recurved, moderately puberulous on both the surfaces but becoming glabrate, usually moderately beset with appressed glandular trichomes ca. 0.1 mm long, 3(5)-nerved from the base, the midvein and the paralleling principal veins often impressed above and elevated beneath, the veinlets usually obscure; petioles glabrous to pilosulose, 1–2(–3) mm long; pedicels 1(–2) per axil, pilosulose and often with inconspicuous, glandular, appressed trichomes distally, sometimes glabrous, (1.0–)1.5–2.5 cm long. *Flowers* with the hypanthium usually moderately spreading pilosulose, occasionally sparingly so or glabrous, usually appressed glandular strigose proximally, subglobose or thickly fusiform to shortly cylindric, 1–1.5(–2) mm long, 1.0–1.5 mm in diameter; calyx limb erect, 1.0–1.6 mm long including the lobes, the lobes 4 or 5, deltoid, acute, 0.5–0.8 mm long, often with a tuft of trichomes at the tip; corolla membranous, (4–) 5–7(–8) mm long, 1.2–2.0(–2.2) mm in diameter, glabrous or sparsely and inconspicuously strigillose or puberulous distally, the lobes 4 or 5, narrowly triangular, acute, erect; stamens usually either 4–5 or 8–10, slightly shorter than the corolla, the filaments slender, pilosulose or glabrous, 2.0–3.5(–4.5) mm long, the anthers 2–3 mm long, the tubules distinct, about as long to almost twice as long as the thecae. *Berry* subglobose to thickly fusiform, pilosulose or glabrous, white or white with a violet tinge at maturity, fleshy, 4–7 mm in diameter; seeds elongate, whitish, the green embryo visible within.

This species ranges from the mountains of southern Mexico and Hispaniola south into northern South America and along the Andes into Bolivia. It ranges east to French Guiana.

It has been customary to recognize at least two species within this complex but *Sphyrospermum majus* can be distinguished from *S. cordifolium* only by its different stamen number. *Sphyrospermum majus* has 4 or 5 stamens and *S. cordifolium* has 8 or 10. This distinction is not absolute as flowers are encountered with all numbers between 4 and 10. This is an unlikely basis for maintaining two separate taxa; suggested differences in pubescence, corolla size and the ratio of tubule to thecae length all intergrade.

Perhaps to be included here under the binomial *S. cordifolium* are several specimens of *Sphyrospermum* with basally tapering, elliptical leaves, but these may represent an undescribed species. The available specimens are incomplete; they are identified below by an asterisk (*).

BOCAS DEL TORO: Mossy forest-cloud forest, E slope of La Zorra to divide, *Kirkbride & Duke* 807 (MO). CHIRIQUÍ: Trail N of Cerro Punta, *Croat* 10520 (MO, SCZ). Rain forest, Bajo Chorro, Boquete, *Davidson* 196 (A, F, MO). Trail beyond Las Nubes to about midway between Cerro Picacho and Cerro Punta, NW of town of Cerro Punta, 1900–2200 m, *Luteyn & Wilbur* 4642 (DUKE, F, MO). Roadsides, pastures and remnants of lower montane wet forest, Bajo Grande, 1–3 km E of the town of Cerro Punta, 2000–2200 m, *Nee* 10036 (DUKE, MO). Cloud forest, Finca Collins, *Stern et al.* 1105 (GH, MO). Boquete Trail, 6 mi E of Cerro Punta, 7000 ft, *Tyson* 7212 (DUKE). Chiriquí Viejo Valley, *White* 82 (GH, NY). W of Las Nubes, 5 km NW of Cerro Punta and towards Cerro Picacho, 2000–2100 m, *Wilbur & Luteyn* 19357 (DUKE), 19402 (DUKE, MO). Valley of the Río Chiriquí Viejo, E of Guadalupe, 6500 ft, *Wilbur et al.* 13039 (DUKE, PMA). COCLÉ: Forest at La Mesa above El Valle, ca. 800 m, *Croat* 25348 (MO). DARIÉN: Between Upper Río Membrillo and Camp 7 on the Construction Road to San Blas, 100–800 m, *Duke* 10928* (MO). Cloud forest and/or mossy forest, Cerro Pirre, 2500–4500 ft, *Duke & Elias* 13795 (MO). Summit of Pico Tacarcuna, 1850 m, *Gentry et al.* 16913 (MO). PANAMÁ: Moist upper regions of

Cerro Campana, 1000 m, *Allen* 2421 (A). Primary forest along El Llano-Cartí-Tupile road 12 mi from Panamerican Highway, *Liesner* 1230 (MO). Cloud forest, Cerro Campana, 850 m, *Luteyn* 3979 (DUKE). Premontane wet forest, El Llano-Cartí Road, 12 km N of Panamerican Highway, 400 m, *Nee & Dressler* 9365* (MO). VERAGUAS: Primary forest on Caribbean slope above Río Primero Brazo, 5 mi NW of Santa Fe, 700–1200 m, *Croat* 23162 (MO). Río Segundo Brazo, 8 km beyond Escuela Agrícola Alto Piedra beyond Santa Fe, *Croat* 25566 (MO). Tropical wet forest on Atlantic slope along Río Dos Bocas 11 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki* 3186 (MO). NW of Santa Fe, 8.8 km from Escuela Agrícola Alto de Piedra, Pacific slope, *Mori & Kallunki* 3937, 3982 (both MO). First branch of Río Santa Maria, S of river along road from Santa Fe, *Witherspoon & Dressler* 8925* (MO).

3. ***Sphyrospermum standleyi*** A. C. Smith, *Brittonia* 1: 210. 1933. TYPE: Costa Rica: Cartago; near Orosi, *Standley* 39622 (US, holotype, not seen; photos DUKE, NY).

Straggly, epiphytic or terrestrial *shrub* 4–6(10) dm tall with subrugose and cinereous branchlets. *Leaves* subcoriaceous, ovate to lance ovate, 4.5–6 cm long, 2–2.8 cm wide, basally rounded or obtuse, apically obtuse, entire, either 5-nerved from the base or 5-plinerved, the midvein and secondary nerves flush above slightly impressed and elevated beneath, the veinlets obscure or slightly raised beneath; petioles subterete, 1.5–2 mm long. *Inflorescence* of axillary or cauliflorous, solitary or paired flowers; pedicels 7–15 mm long, swollen distally. *Flowers* with the hypanthium campanulate, strigillose with dark trichomes 0.1 mm long but neither pilose nor puberulent, slightly 4-angled, 1–1.5 mm long, 1.5 mm in diameter, the calyx limb suberect, 0.8 mm long including the lobes, the lobes 4, apiculate; corolla membranaceous, short cylindrical, 2–2.3 mm long, 1 mm in diameter, the corolla lobes 4, deltoid, acute, ca. 0.3 mm long; stamens 4, slightly shorter than the corolla, the filaments stramineous, ca. 1.2 mm long, the anthers membranaceous, ca. 1 mm long, the tubules as long as the anther sacs. *Berry* white, subglobose, 3–5 mm in diameter.

This little collected and poorly understood species is known from a few collections made in central Costa Rica and in eastern Panama.

DARIÉN: Cerro Tacarcuna massif on westernmost ridge and Pico Tacarcuna, 1650–1800 m, *Gentry et al.* 16914 (NY).

4. ***Sphyrospermum tuberculatum*** Wilbur & Luteyn.⁶ TYPE: Panama, *Witherspoon* 8830 (MO, holotype).

Epiphytic *shrub*; branches terete, striate, fissured, grayish, glabrous. *Leaves* coriaceous, broadly elliptic, 1.8–5.1 cm long, 1.2–2.8 cm wide, basally rounded to obtusely cuneate, apically rounded, entire, glabrous but inconspicuously glandular strigillose on both surfaces, more so beneath, obscurely 3-plinerved; petioles glabrous, 2–3 mm long. *Inflorescence* of solitary or paired flowers in the leaf axils; pedicels pendent, arching in both young and older fruit, 6–8 mm

⁶ *Sphyrospermum tuberculatum* Wilbur & Luteyn, sp. nov. Frutex epiphyticus. Lamina foliorum coriacea, elliptica, apice et basi rotundata, 1.8–5.1 cm longa et 1.2–2.8 cm lata, margine integra; petiolo glabro, 2–3 mm longo. Hypanthia tuberculata, ca. 2.5 mm alta et 2–2.2 mm diametro; lobis calycis 5, glabris, 0.4–0.5 mm longis.

long, with dense bulbous based trichomes at least distally; bract triangular, appressed, ca. 0.6 mm long, bracteoles triangular, alternate, 0.3–0.5 mm long, nearly basal. *Flowers* with the hypanthium densely tuberculate with bulbous-based, glandular protuberances, ca. 2.5 mm high, 2–2.2 mm in diameter; calyx limb glabrous, erect to slightly spreading, 0.5–0.7 mm long including the lobes, the lobes 5, erect, triangular, glabrous, 0.4–0.5 mm long. *Fruit* a globose, densely tuberculate white berry; seeds cuneiform with a striate, transparent (when dry) outer layer exhibiting the green embryo within.

This new species is known from a single specimen consisting of three twigs. The dense hypanthial covering of tuberculae is like that of no other species of *Sphyrospermum* known to us.

VERAGUAS: 2 km N of Cerro Tute, Witherspoon 8830 (MO).

17. THEMISTOCLESIA

Themistoclesia Klotzsch, *Linnaea* 24: 41. 1851. LECTOTYPE: *T. pendula* Klotzsch.

Straggly to bushy, often epiphytic *shrubs* or *shrublets*. *Leaves* subcoriaceous to coriaceous, occasionally fleshy, alternate, shortly petiolate; venation obscure. *Inflorescence* axillary, racemose or solitary with one to several flowers, pedicels usually short, subtended by small bracts and bearing usually inconspicuous bracteoles. *Flowers* with the hypanthium continuous with the pedicel, obconic or short cylindric, narrowly 5-winged to the sinuses or bluntly angled, the calyx limb erect to slightly spreading, the 5 lobes acute to acuminate, minute to well developed; corolla ovoid to cylindric, the lobes 5; stamens 4–5 or 8–10, equal or alternately slightly unequal, more than $\frac{1}{2}$ as long as the corolla and often about as long as the corolla tube, the filaments distinct, slender and terete to somewhat flattened at the base, the anthers inserted medially or almost basally, the walls smooth, nearly equal to or only about $\frac{1}{2}$ as long as the tubules, the tubules 1 or 2, if 2, often completely separate, dehiscing by short, introrse clefts; style filiform, about as long as the corolla. *Berry* with numerous small seeds; the green embryo clearly visible through the surrounding tissue.

Themistoclesia is a genus of about 25 species ranging from Costa Rica and Panama through the Andes from Venezuela and Colombia into Peru.

- a. Staminal tubules 1 per anther with a single introrse cleft; hypanthium distinctly 5-winged; leaves apically obtuse 3. *T. pentandra*
- aa. Staminal tubules 2 per anther, the tubules either separate or united but with 2 introrse clefts; hypanthium bluntly 5-angled, not winged; leaves apically acute or acuminate.
 - b. Corolla 2.5–3.5 mm long; leaves less than 1.9 cm long, basally tapering or cuneate 4. *T. smithiana*
 - bb. Corolla 5–6 mm long; leaves more than 2 cm long, basally rounded, subtruncate or subcordate.
 - c. Bracteoles ovate to hemispheric, completely concealing the glabrous pedicel; corolla cylindric, pilosulose throughout; stamens 5 mm long, filaments pilosulose, anther basally minutely appendiculate 1. *T. costaricensis*
 - cc. Bracteoles awl-shaped, never concealing the pilosulose pedicel; corolla

urceolate, pilosulose distally; stamens 2.5 mm long, filaments glabrous, anther without basal appendage 2. *T. horquetensis*

1. ***Themistoclesia costaricensis*** Luteyn & Wilbur, Brittonia 29: 265. 1977.
TYPE: Costa Rica, *Luteyn et al.* 4407 (DUKE, holotype; F, MO, NY, isotypes).

Pendent, epiphytic *shrub* with branches to 0.5 m long; stems terete, minutely striate, tan to reddish brown when dry, hispidulous with reddish brown trichomes 0.6–0.8 mm long, glabrate with age. *Leaves* distichous, flat or concave, ovate, (1.6–)2–2.5 cm long, (0.8–)1–2 cm wide, basally rounded or subcordate, apically acute or short acuminate, entire, hispidulous above especially near the margins, glabrous beneath, brown above and olive green or light brown beneath when dry; venation obscurely 5-plinerved, the midrib slightly impressed proximally, raised distally above, slightly impressed but inconspicuous beneath, the lateral nerves and the veinlets slightly raised but inconspicuous above, totally obscure beneath; petiole subterete, densely puberulous to pilosulose, 1–1.5 mm long. *Inflorescence* of axillary, solitary flowers with 4 minute basal inflorescence bracts; floral bract ovate, ciliate, ca. 1.5 mm long; pedicel terete, glabrous, 1–2 mm long, completely concealed by the bracteoles; bracteoles 2, ovate to hemispheric, distally hispidulous. *Flowers* with the hypanthium glaucous, copiously pilosulose with translucent or reddish tinged trichomes 1–1.2 mm long, the tube obconic, bluntly 5-angled, ca. 3 mm long; calyx limb 1–1.5 mm long including apiculate lobes; corolla cylindric, narrowed at the throat, 5–6 mm long, ca. 2.2 mm in diameter near the base, pilosulose throughout, white, the lobes ca. 1 mm long; stamens 10, ca. 5 mm long, the filaments alternately 2.8–3 mm and 3–3.2 mm long, pilosulose over the entire length, the anthers ca. 2.5 mm long, the tubules slightly longer than the thecae, the theca with a minute, 0.1 mm long, fingerlike appendage protruding from the base; style 5–6 mm long, glabrous. *Berry* not seen.

Themistoclesia costaricensis is known from Serranía del Darién and from Costa Rica. The identity of the Panamanian specimen is not certain as the material is immature, and there are discrepancies between it and specimens from the type locality along the Río Grande de Orosi in central Costa Rica. These differences include cauline trichomes 0.8–1.2 mm long vs. 0.6–0.8 mm long, leaves to 3 cm long vs. 1.6–2.5 cm long, bracts and bracteoles glandular fimbriate vs. ciliate, and pedicels sparsely pilosulose vs. glabrous.

DARIÉN: summit of Pico Tacarcuna, highest point of the Serranía del Darién, 1850 m, *Gentry et al.* 16911 (NY).

2. ***Themistoclesia horquetensis*** Luteyn & Wilbur, Brittonia 29: 266. 1977.
TYPE: Panama; Chiriquí, S slope of Cerro Horqueta, 2,200 m, *Wilbur et al.* 13491 (DUKE, holotype).

Epiphytic *shrub* ca. 5 dm tall; stems subterete or bluntly angled, minutely striate but becoming smooth, glaucous, pale reddish brown when dry, hispidulous with translucent trichomes 0.2–0.3 mm long, glabrous with age. *Leaves* distichous, ovate, (2.5–)3–4.5 cm long, 1.5–2.5 cm wide, basally broadly rounded or subtruncate, apically short acuminate, apiculate, entire, obscurely short pilose

above, especially near the margins, glabrous beneath, pale green above, brown beneath when dry but with a pale greenish brown area 1 mm broad along the entire margin; venation 3(-5)-plinerved, the nerves obscure but slightly impressed above, only the midrib slightly raised beneath; petiole subterete, flattened above, 2-3 mm long and 1 mm diameter, hispidulous with translucent trichomes 0.2-0.3 mm long. *Inflorescence* of axillary, solitary flowers, bracts 2-4, minute, basal; floral bract ovate, ciliate, 0.3-0.5 mm long; pedicels angled, striate, glaucous, hispidulous, 1.5-2.5 mm long; bracteoles awl-shaped, ciliate, ca. 0.5 mm long, supramedial. *Flowers* with the hypanthium glaucous, sparsely hispidulous with translucent hairs ca. 0.2 mm long, the tube obconic, bluntly 5-angled, 2-3 mm long; calyx limb 1.5-1.7 mm long including the apiculate lobes; corolla urceolate, strongly constricted at the throat, 5-5.5 mm long, ca. 2.2 mm diameter near the base, glabrous below, the upper part of the throat and the lobes hispidulous, the lobes ca. 0.5 mm long; stamens 10, 2.5 mm long, the filaments alternately 1.5 and 2 mm long, glabrous, the anther 1-1.2 mm long inserted near the base, the tubules equaling the thecae; style ca. 3.5 mm long, glabrous. *Berry* ca. 5 mm in diameter.

This species is known only from the holotype.

CHIRIQUÍ: S slopes of Cerro Horqueta, N of Boquete, 2200 m, *Wilbur et al.* 13491 (DUKE).

3. ***Themistoclesia pentandra*** Sleumer, Bot. Jahrb. Syst. 71: 392. 1941. TYPE: Costa Rica, Prov. de Cartago, La Estrella, *Standley* 39374 (US, holotype).

Epiphytic, often slender and straggly *shrub* 3-6(-15) dm tall with ascendent branches; stems terete, striate, fissured, grayish to brown or reddish brown, moderately to densely spreading short pubescent or pilosulose with hyaline trichomes 0.2-0.6 mm long, glabrate with age. *Leaves* spirally arranged, elliptic to oblong elliptic, (1.5-)2.0-3.5(-4.5) cm long, (0.8-)1.2-2.0(-2.5) cm wide, basally cuneate, less commonly rounded, apically acute to obtuse, entire, moderately but inconspicuously spreading pilosulose to puberulous on both the surfaces when young, becoming glabrate or more sparsely pubescent, the lower surface also inconspicuously moderately glandular strigillose, obscurely 3-5-plinerved, the midvein and the principal veins slightly elevated above and beneath, the lateral veins obscurely reticulate on both the surfaces; petiole flattened above, pilosulose to puberulous, rugose, 1-2(-3) mm long. *Inflorescence* of axillary, solitary or very rarely paired flowers; bracts 2 or 4, appressed, triangular 1-1.5 mm long; bracteoles 2, appressed, lanceolate, puberulous 1.2-1.5 mm long; pedicels terete, puberulous 1.5-2.5 mm long. *Flowers* with the hypanthium 3.5-4 mm long, conspicuously 4-5-winged, the wings conspicuously ciliate with hyaline trichomes 0.2-0.4 mm long, these trichomes occurring elsewhere on the surface, the surface of the hypanthium sparingly to moderately beset with minute, glandular trichomes; calyx limb 0.8-1.0 mm long including the minute apiculate lobes; corolla sharply pentangular, tapering sharply to the throat, 3-4.5 mm long, basally 2.0-2.5 mm in diameter, moderately hyaline pilosulose throughout, both internally and externally, light orange with a pale

yellow tip, the lobes 4–5, narrowly triangular, acute, 1.0–1.5 mm long, erect or the tips slightly spreading; stamens 5–10, 3.2–3.5 mm long, equal or nearly so, about as long as the corolla tube; filaments glabrous or sparingly ciliate, ca. 1.5 mm long, flattened basally, the anther sacs attached medially, the thecae slightly granular, 1.0–1.2 mm long, the tubules smooth, conical, 1.5–1.8 mm long; stigma truncate, the style 3–3.5 mm long or about as long as the corolla tube. *Fruit* 4–5-winged, the wings 1–2 mm wide, pale greenish, 5–7 mm long.

Themistoclesia pentandra has been rarely collected and specimens seen have been incomplete. It is possible that more than one species is included under this binomial. Most recent collections have 8 or 10 stamens while the original description and indeed the specific epithet indicates 5. The inclusion of *Duke & Elias* 13688 from Darién is especially suspect due to the following differences from all other specimens of *T. pentandra*; the calyx is glabrous rather than ciliate, the corolla is glabrous externally and minutely papillose or short puberulous within in contrast to being externally and internally pilosulose, and its stamens, including the filaments, thecae and tubules are all shorter. These differences are significant but we are reluctant to name another species based upon a single, rather incomplete specimen.

CHIRIQUÍ: N of San Félix on Cerro Colorado Copper Mine road along continental divide, 5000–5500 ft, *Mori & Kallunki* 5984 (MO). COCLÉ: Cloud forest on slopes of Cerro Pilón near El Valle, 700–900 m, *Duke* 12080, 12085 (both MO). Tropical wet forests, La Mesa, 4 km N of El Valle, 875 m, *Nee & Hale* 9612 (MO). DARIÉN: Cloud forest and/or mossy forest, Cerro Pirre, 2500–4500 ft, *Duke & Elias* 13688 (DUKE, MO).

4. ***Themistoclesia smithiana*** (Standley) Sleumer, Bot. Jahrb. Syst. 71: 392. 1941.

Vaccinium smithianum Standl., Fieldiana, Bot. 18: 833. 1938. TYPE: Costa Rica, *Standley & Valerio* 51858 (F, holotype; US, isotype).

Pendent to spreading, epiphytic *shrublet* mostly 2–3(–4.5) dm tall; stems terete, slender, brown or reddish brown to grayish when dry, densely to moderately pilosulose with hyaline trichomes 0.2–0.5 mm long, maturing to glabrate. *Leaves* thickly coriaceous, distichous, concave, lanceolate to ovate lanceolate, (0.7–) 1.0–1.5(–1.8) cm long, (3.0–) 6.0–8.0 mm wide, basally acute to rounded, apically acute to acuminate, entire, inconspicuously but copiously pilosulose above when young becoming glabrate, the trichomes slender, spreading, ca. 0.2 mm long, beneath glabrous except for reddish brown, minute, glandular trichomes 0.1 mm long or less; venation obscure above except the midvein sunken above and completely obscured beneath; petiole terete, densely hispidulous, 0.5–1.5 mm long. *Inflorescences* of axillary, solitary flowers; bracts several, basal; floral bract ovate, pilosulose, ca. 0.8 mm long; pedicel terete, pilosulose, 1.0–1.2 mm long; bracteoles linear to linear oblong, reddish brown, pilosulose, 0.4–0.6 mm long. *Flowers* with the hypanthium copiously pilosulose with hyaline trichomes 0.3–0.6 mm long, the tube obconic, terete, ca. 2.5 mm long at anthesis; calyx limb ca. 0.7 mm long, the triangular, acute lobes 1.2–1.5 mm long; corolla pale yellow to pale greenish white or white, terete or obscurely 5-lobed, broadly ovoid, abruptly narrowed at the throat, 3–3.5 mm long, 2.5–3 mm in diameter near the base and 0.8–1.0 mm in diameter at the throat,



FIGURE 17. *Themistoclesia smithiana* (Standl.) Sleumer.—A. Habit ($\times \frac{4}{5}$).—B. Flower ($\times 8$). [After Mori & Kallunki 5910 (MO).]

glabrous for the basal $\frac{1}{2}$, pilosulose distally, the lobes linear oblong, 0.5–0.8 mm long, erect or weakly flaring; stamens 10, equal, ca. 2.5 mm long or about as long as the corolla tube, the filaments slender, terete, glabrous, attached medially to the back of the anther sac, the anther ca. 1.5 mm long including the tubules, smooth, the 2 separate tubules on each anther 0.8–1.0 mm long and dehiscing by an introrse cleft ca. 0.6 mm long, the thecae smooth, 0.6–0.8 mm long, straight; style ca. 3 mm long. *Berry* inconspicuously angled, 5–7 mm long, ca. 4 mm in diameter, bluish.

The distinctive but easily overlooked *T. smithiana* is known only from central Costa Rica and from western Panama.

CHIRIQUÍ: Cloud forest N of San Félix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine road along the continental divide, *Mori & Kallunki* 5910 (MO). VERAGUAS: On ridgetop in cloud forest, Cerro Tute 10 km NW of Santa Fé, above 1000 m, *Mori et al.* 7592 (MO).

18. THIBAUDIA

Thibaudia Ruiz & Pavón ex St. Hil., Expos. Fam. 1: 362. 1805. LECTOTYPE: *T. mellifera* Ruiz & Pavón ex St. Hil.

Eurygania Klotzsch, Linnaea 24: 15, 26. 1851.

Epiphytic or terrestrial *shrubs*. *Leaves* coriaceous or subcoriaceous, pinnately veined or plinerved, petiolate. *Inflorescence* axillary or terminal, subfasciculate, racemose or paniculate with few to many flowers borne on deciduously bibracteolate pedicels articulated with the flowers or rarely continuous (in one South American section). *Flowers* with the hypanthium short cylindric or campanulate, wingless or occasionally narrowly 5-angled to the sinuses (South America); calyx limb erect to slightly spreading distally, the lobes 5, triangular, subacute; corolla subcylindric, occasionally 5-angulate, the lobes 5, triangular or oblong, subacute; stamens 10, equal, often nearly as long as the corolla, the filaments distinct (Central America) or connate (some South American species), the anthers dorsally attached near the bases, firm or membranous, the thecae smooth or slightly granular, the tubules as long as the anther sacs or rarely twice as long, opening by elongate introrse clefts; style filiform, as long as the corolla or slightly exserted; ovary inferior. *Fruit* a berry.

Thibaudia is a genus of about 60 species with one species in Panama and Costa Rica and the others ranging from Colombia to Peru and eastward to Mt. Roraima on the Venezuela-Guayana border.

1. *Thibaudia costaricensis* Hoerold, Bot. Jahrb. Syst. 42: 311. 1909.—FIG. 18.

Usually epiphytic *shrubs*; branches elongate to 2 m long; branchlets terete, cinereous, glabrous. *Leaves* chartaceous or thin coriaceous, oblong or lanceolate oblong, to elliptic, (10–)12–24 cm long, (1.7–)3.5–5(–7.5) cm wide, basally cuneate, apically caudate acuminate, marginally entire and slightly revolute, superficially glabrous or with inconspicuous glandular strigillose trichomes on both the surfaces, 5-plinerved, the secondary nerves originating near the base, the midvein

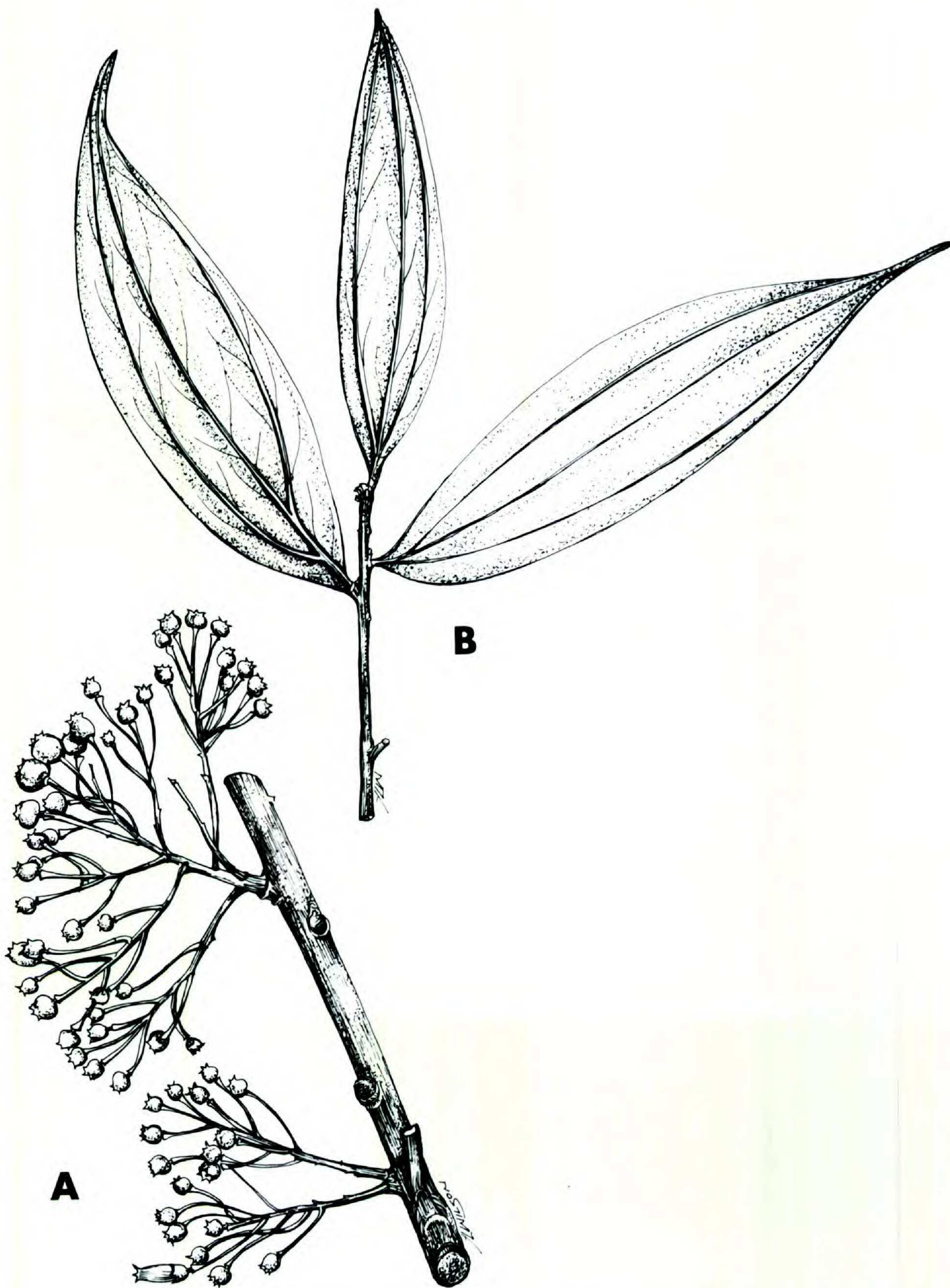


FIGURE 18. *Thibaudia costaricensis* Hoerold.—A. Inflorescences ($\times \frac{3}{5}$).—B. Leafy twig ($\times \frac{3}{5}$). [After Wilbur & Stone 8633 (DUKE), Costa Rica.]

impressed above and prominently raised beneath, the veinlets reticulate and slightly raised on both the surfaces; petioles glabrous, 2–3(–4) mm long. *Inflorescences* axillary or cauliflorous, numerous, racemose, or paniculate, 15–30-flowered, the rachis slender, 2–5 cm long, laxly and sparsely puberulous or gla-

brous; pedicel reddish or pinkish, subterete, glabrous or puberulous, distally slightly swollen, 10–16 mm long; bract minute, deciduous, 1–1.5 mm long; bracteoles 2, submedial, deciduous 0.8–1.2 mm long with a sharply delineated disarticulation groove at the base of the flower. *Flowers* with the hypanthium rugose, sparsely puberulous or glabrous, pinkish to roseate, ca. 2 mm long, 2.5 mm in diameter, campanulate, the calyx limb 1–2 mm long including the lobes, erect or spreading, the lobes acute, 0.5–1 mm long, sometimes cartilaginous; corolla tube 9–10 mm long, cylindric, white, 3–3.5 mm in diameter, slightly contracted at the base and at the throat, the lobes 1–1.5 mm long; stamens 10, ca. 7 mm long, equal or almost so; filaments brown, membranous, firmly connate into a glabrous tube 2–3 mm long; anther sacs smooth to slightly granular, ca. 2 mm long, the tubules wide, flexible, completely free ca. 3 mm long opening introrsely by elongate, oval clefts about $\frac{1}{2}$ as long as the tubule; stigma broadly peltate, ca. 1 mm in diameter, the style exerted 1–2 mm at maturity.

This distinctive and relatively uniform species is the only representative of the genus in Central America. It is endemic to the mountains of western Panama and central Costa Rica.

BOCAS DEL TORO: Robalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen* 4808 (GH, MO, NY, US). CHIRIQUÍ: Bajo Chorro, Boquete District, 6000 ft, *Davidson* 380 (A, F, MO, US). Along path in rain forest, Boquete Region, 6500 ft, *Hagen* 2023 (A, NY). Premontane rain forest between Pinola and Quebrada Hondo toward summit, *Kirkbride & Duke* 880 (MO, NY). Bajo Chorro trail towards Boquete from Cerro Punta, 7000 ft, *Luteyn* 3057, 3063 (both DUKE). Heavily forested slopes along ridge on the W side of Cerro Horqueta, 1700–1800 m, *Luteyn* 3760 (DUKE).

19. VACCINIUM

Vaccinium L., Sp. Pl. 1: 349. 1753; Gen. Pl., ed. 5. 166. 1754. LECTOTYPE: *Vaccinium myrtillus* L.

Oxycoccus Hill, Brit. Herb. 324. 1756. TYPE: *Vaccinium oxycoccus* L.

Polycodium Raf., Amer. Monthly Mag. & Crit. Rev. 2: 266. 1818 and 4: 189. 1819.

Batodendron Nutt., Trans. Amer. Philos. Soc. II. 8: 261. 1843. TYPE: *B. arboreum* (Marshall) Nutt. (= *V. arboreum* Marshall).

Picrococcus Nutt., Trans. Amer. Philos. Soc. II. 8: 262. 1843. LECTOTYPE: *P. stamineum* (L.) Nutt. = *Vaccinium stamineum* L.

Cyanococcus (A. Gray) Rydb., Fl. Rocky Mts. 645, 1065. 1917. TYPE: *C. pensilvanicus* (Lam.) Rydb. (*pennsylvanicus*) (= *V. angustifolium* Ait.).

Herpothamnus Small, Man. S.E. Flora 1017. 1933. TYPE: *H. crassifolius* (Andr.) Small = *Vaccinium crassifolium* Andr.

Hugeria Small, Fl. S.E. U.S. 896. 1903. TYPE: *Hugeria erythrocarpa* (Michx.) Small (= *Vaccinium erythrocarpum* Michx.)

Rhodococcum (Rupr.) Avorin, Bot. Zurn. SSSR. 43: 1721. 1958. TYPE: *Rhodococcum vitis-idaea* (L.) Avorin (= *Vaccinium vitis-idaea* L.).

Shrubs or rarely *trees*, often rhizomatous. *Leaves* persistent or deciduous, entire or serrate, pinnately veined or rarely plinerved; petioles short. *Inflorescences* racemose, developing from the buds of the previous season, rarely only 1–2 flowered, the flowers borne in the axils of the bracts or the leaves; pedicels usually bibracteolate, either articulated or continuous. *Flowers* with the hypanthium cylindric to globose; calyx lobes (4–)5, rarely obsolete; corolla gamopetalous, white, greenish, red or yellowish, cylindric, urceolate or campanulate,

the lobes 4–5, rarely parted almost to the base; stamens 8 or 10, the anthers lacking awns and with or without dorsal spurs, tapering upward into tubules and opening by a terminal pore or rarely an oblique cleft; pollen in tetrads and without viscin strands; stigma small, simple or somewhat capitate, the ovary completely or partly inferior, 4–5(–falsely 10)-locular, the placentation axile. *Berry* 5 to many seeded, crowned by the persistent calyx lobes and capped by the conspicuous nectariferous disc.

Vaccinium is a genus of perhaps 300 species primarily of the Northern Hemisphere, mostly montane in the tropics. The genus as usually interpreted is diverse and this diversity is amply exhibited by the few representatives found in Central America.

Literature:

Sleumer, H. 1936. Die Arten der Gattung *Vaccinium* L. in Zentral und Südamerika. Notizbl. Bot. Gart. Berlin-Dahlem 13: 111–140.

Standley, P. C. 1920–26. Trees and shrubs of Mexico. Contr. U.S. Natl. Herb. 23: 1–1721.

- a. Leaves crenate serrulate; corolla white or white tinged with pink or red; flowers borne in a secund raceme; anthers spurred; calyx and corolla lobes 4 1. *V. consanguineum*
- aa. Leaves entire; corolla reddish or pale greenish yellow; flowers solitary in the axils of the leaves or borne in an umbelliform cluster; anthers spurless; calyx and corolla lobes 4 or 5.
 - b. Corolla 4-lobed, red or reddish purple; stamens 8; shrublets creeping, vinelike, closely clasping the bark; hypanthium and pedicel continuous (nonarticulate); flowers solitary 2. *V. dissimile*
 - bb. Corolla 5-lobed, mostly pale greenish yellow to yellow but often tinged with pink; stamens 10; erect shrubs or trees, or, if epiphytic, neither creeping nor closely clasping the bark; hypanthium and pedicels jointed (articulate); flowers in corymbose or umbellate racemes.
 - c. Calyx lobes 5–6 mm long; principal veins of leaves moderately spreading hirsute beneath; hypanthium and calyx lobes both hirsute and with glandular, capitate protuberances 4. *V. jefense*
 - cc. Calyx lobes 4 mm or less long; principal veins of leaves at most puberulent or glandular strigillose beneath; hypanthium and calyx lobes glabrous to inconspicuously puberulous.
 - d. Calyx lobes 2–3.5 mm long; staminal tubules ca. 1 mm long 3. *V. floccosum*
 - dd. Calyx lobes 1 mm long or less; staminal tubules 3 mm long or longer.
 - e. Staminal tubules 3.5–5.5 mm long, each dehiscing by a terminal truncate or slightly inwardly facing pore; Chiriquí 5. *V. poasanum*
 - ee. Staminal tubules 3.0–3.2 mm long, each dehiscing by a lateral cleft 2–2.5 mm long; Veraguas 6. *V. santafeënsis*

1. *Vaccinium consanguineum* Klotzsch, Linnaea 24: 64. 1861. TYPE: Panama, Warscewicz (B, not seen and presumably destroyed; photo seen, MO).

V. irazuense Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 138. 1934. TYPE: Costa Rica: Lavafelder des Irazú, C. Hoffman 140 (B, not seen and presumably destroyed but fragments seen at US).

V. consanguineum var. *irazuense* (Sleumer) Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 13: 126. 1936.

Shrubs or small *trees* (0.5–)1–3(–4) m tall, often compact and densely bushy with stiff, rigid, glabrous to densely puberulent branchlets. *Leaves*

pinnately veined, persistent, glabrous or with scattered glandular trichomes beneath and moderately puberulous along the midvein; shallowly serrulate with teeth mostly (1-)2-4 mm apart, each tooth often tipped with a darkish glandular callosity, marginally callose thickened, (1.0-)1.5-3(-4.6) cm long, 5-12(-18) mm wide, usually 2-3 times as long as wide, mostly narrowly to broadly elliptic, occasionally oblong, usually tapering to an acute apex and base; petioles 1.5-3 mm long, glabrous or puberulent. *Inflorescence* an axillary raceme, mostly 1-4 cm long; rachis sharply angled, puberulent; bracts scarious, slightly puberulent or ciliate, ovate to oblong, 2-3 mm long; pedicels puberulent, 1-2 mm long; bractlets subopposite, ovate to oblong, scarious, ciliate but otherwise glabrous, entire to sparingly irregularly and minutely toothed, 1.5-3 mm long. *Flowers* with the hypanthium sharply articulated with the pedicel, campanulate, glabrous, 1-1.6 mm long; calyx limb 0.5-0.7 mm long, the lobes 4, deltoid to broadly ovate, apically ciliate but otherwise glabrous, 0.8-1.5 mm long; corolla cylindric, 5-7.5 mm long, glabrous, creamy white with tinges of red or pink, the tube 4-6 mm long, 3-4 mm in diameter, the corolla lobes 4, oblong, 1-1.7 mm long; stamens 8, the filaments 3-4 mm long, ciliate, the anthers granular papillate, the thecae 1.5-1.8 mm long, each sac with a tubule and 2 spurs, the tubule 1.2-1.8 mm long dehiscing by an introrse cleft 0.5-0.7 mm long, the spurs slender, horn-like, ascendent, originating from near the apex of the thecae, 0.2-0.6 mm long. *Berry* reddish to blackish purple at maturity, globose, 5-6 mm in diameter.

This species was included by Standley (1920-26, p. 1101-1102) as part of the woody flora of Mexico but its presence north of Costa Rica was questioned by Sleumer (1936) and the species was not included by Standley & Williams in the Flora of Guatemala (Fieldiana, Bot. 24: 120-127. 1966). It apparently is restricted to the mountains of western Panama and Costa Rica.

CHIRIQUÍ: Forested ridges S of Finca Lerida, 6000-7000 ft, *Allen* 4768 (F, GH, MO, NY, US). Summit and SW face of Cerro Copete, 9000 ft, *Allen* 4894 (MO, US). Volcán Barú, on E slopes, along road 1 mi from summit, 3000 m, *Croat* 34917 (MO). Road up E slope of Volcán Barú, 8 mi from Boquete, 2300-2400 m, *Croat* 35001 (MO). Roadside, Potrero Muleto to summit of El Barú, *D'Arcy* 10152, 10170 (both DUKE, MO). E slope of Volcán de Chiriquí, WNW of Boquete, 1900-2000 m, *Davidse & D'Arcy* 10165 (DUKE, MO, NY). Oak forest at 2400 m, E slopes of Volcán de Chiriquí, WNW of Boquete, *Davidse & D'Arcy* 10204 (DUKE, MO, NY). Volcán de Chiriquí, 7000 ft, *Davidson* 868 (A, F, MO, US), 901 (F). Potrero Muleto, Volcán de Chiriquí, 10500 ft, *Davidson* 1034 (A, F, MO), *Davidson* 1056 (A, F, US). Llanos near El Hato del Volcán on road to Cerro Punta, 6000 ft, *Luteyn* 3050 (DUKE, MO). Premontane cloud forest along ridge E of Cerro Horqueta, 1700-1900 m, *Luteyn & Wilbur* 4602 (DUKE). Trail to summit, W slopes of Volcán de Chiriquí, 2500-3400 m, *Mori & Kallunki* 5743 (DUKE, MO). N of San Félix at Chiriquí-Bocas del Toro border on Cerro Colorado copper mine road along continental divide, 5000-5500 ft, *Mori & Kallunki* 5808 (DUKE, MO). Potrero Camp, Chiriquí Volcano, 2800-3000 m, *Pittier* 3077 (F, US). Near peak, Volcán de Chiriquí, 11900 ft, *Terry* 1316 (F), 1332 (A, F). W slope of El Barú above 10000 ft, *Tyson & Loftin* 6133, 6138, 6155 (all DUKE). Valley of the upper Rio Chiriquí Viejo, *White* 16 (MO). Slopes of Volcán Chiriquí, 9800 ft, *Wilbur et al.* 11027 (DUKE, MO). Upper end of lava field NE of El Hato del Volcán, 6200 ft, *Wilbur et al.* 17218 (DUKE). Finca Lerida, 1750 m, *Woodson & Schery* 229 (GH, MO, NY). Casita Alta to Cerro Copete, 2300-3300 m, *Woodson & Schery* 372 (GH, MO, NY). Potrero Muleto to Summit, Volcán de Chiriquí, 3500-4000 m, *Woodson & Schery* 388 (GH, MO, NY); *Woodson & Schery* 435 (GH, MO, NY). Casita Alta, Volcán de Chiriquí, 1500-2000 m, *Woodson et al.* 813 (A, NA, NY). Loma Larga to summit, Volcán de Chiriquí, 2500-3380 m, *Woodson et al.* 1050 (A, MO, NA, NY), 1071 (A, NA, NY), 1092 (MO).

2. ***Vaccinium dissimile*** Blake, J. Bot. 53: 271. 1915. TYPE: Costa Rica: Prov. de San José; La Palma, 1550 m, *Tonduz* (C.R. Nat. Herb. #12546) *J. Donnell Smith* 7380 (BM and K, syntypes neither seen; US, isotype).—FIG. 19.

Disterigma dissimile (Blake) Blake, Proc. Biol. Soc. Wash. 35: 120. 1922.

Creeping, epiphytic, viney *shrublets* with stems interwoven amongst the epiphytic bryophytes; stems wiry, perhaps to a meter long, 1–1.5 mm in diameter, the young stems densely spreading puberulent, glabrous in age. *Leaves* ovate, lance ovate or narrowly to broadly elliptic, coriaceous, entire, revolute, mostly 1.5–3.0(–4.0) cm long, 8–15(–18) mm wide, glabrous above and beneath or beneath sparingly to moderately beset with dark glandular, appressed trichomes 0.1–0.2 mm long, apically acute and basally rounded to cuneate; petioles 1–2 mm long, puberulent. *Inflorescences* of axillary, solitary flowers, pedicels 1–1.5 (–4 or fide A. C. Smith to 8) mm long, the bracteoles basal, 2, ovate to broadly oblong, opposite, obtuse to broadly rounded, puberulent, 0.8–1 mm long and nearly as wide. *Flowers* with the hypanthium campanulate, 2.2–2.8 mm long, densely hirsutulous with hyaline trichomes 0.1–0.2 mm long, the calyx lobes 4, broadly deltoid, acute, 0.7–0.8 mm long, moderately to densely hirsutulous; corolla red, campanulate, sparingly and inconspicuously beset with spreading, gland-tipped trichomes 0.1–0.2 mm long, the tube 7–9 mm long, 6–7 mm in diameter at the apex or the broadest point, the lobes 4, acutely deltoid, 1.5–2 mm long, erect; stamens 8, the filaments 3.5–4.0 mm long, sparsely pilose, elliptical, tapering both to the base and the apex where about 0.5 mm wide, the anthers medifixed, spurless, 2–2.5 mm long, conspicuously papillose granular, each sac tapering into an erect tubule 2–2.5 mm long which opens by an introrse cleft 0.5–0.7 mm long; ovary 4-loculate. *Berry* not seen.

This species is known from the cloud forests of parts of Costa Rica, Panama, and northwestern Colombia, but the plant is easily overlooked. Blake placed this species in the genus *Disterigma*, but Smith (1933) disagreed since the “pedicellary bracts, which are much smaller than those of typical species [of *Disterigma*], do not clasp the tube,” “the pedicels themselves are usually longer than those described by Blake (up to 8 mm long), and the plant does not have the compact close-leaved habit of *Disterigma*.” Sleumer (1936) established the monotypic section *Pseudodisterigma* Sleumer of *Vaccinium* for this species. It seemingly rests comfortably in neither genus but its proper placement must await generic reappraisal of the vaccinioid ericads.

BOCAS DEL TORO: Between Q. Gutierrez and E slope of La Zorra, headwaters of Río Mali, Chiriquí Trail, *Kirkbride & Duke* 729 (MO). CHIRIQUÍ: Cloud forest, Cerro Colorado, 50 km N of San Félix, ca. 1400 m, *Dressler* 5086 (DUKE, MO). COCLÉ: Cerro Pajita, hills N of El Valle 1100 m, *Allen* 3782 (MO). La Mesa above El Valle, 800 m, *Croat* 25431 (MO). Summit of Cerro Pilón above El Valle de Antón, ca. 2700 ft, *Dwyer* 4488 (MO). La Mesa, 5 mi N of El Valle, 2500 ft, *Tyson et al.* 2443 (DUKE). PANAMÁ: Premontane rain forest, Cerro Jefe, along trail on ridge running NE from summit, 1000 m, *Mori et al.* 3756 (MO). Cerro Jefe, new road leading N from summit, *Witherspoon* 8526 (DUKE, MO). VERAGUAS: Tropical wet forest, Atlantic slope, 11 km from Escuela Agrícola Alto de Piedra along Río Dos Bocas, *Mori & Kallunki* 3177 (MO). NW of Santa Fé, 8.8 km from Escuela Agrícola Alto de Piedra, Pacific slopes, *Mori & Kallunki* 3939 (MO).

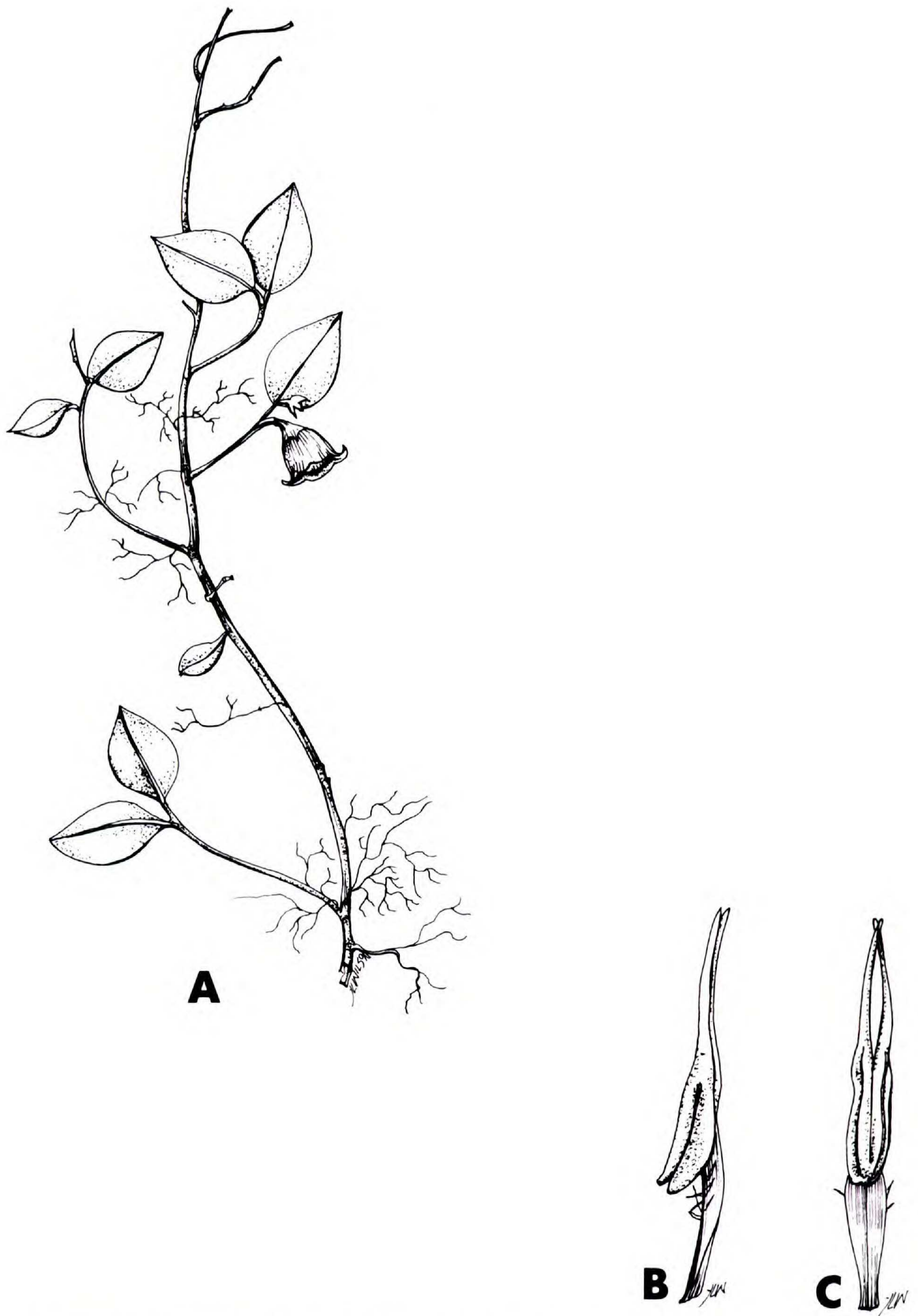


FIGURE 19. *Vaccinium dissimile* Blake.—A. Habit ($\times 1$).—B–C. Stamens.—B. Lateral view ($\times 8\frac{1}{4}$).—C. Ventral view ($\times 8\frac{1}{4}$). After Wilbur 16898 (DUKE).]

3. ***Vaccinium floccosum*** (L.O. Wms.) Wilbur & Luteyn, *Brittonia* 29: 272. 1977.

Hornemannia floccosa L.O. Williams, *Brittonia* 18: 248. 1966. TYPE: Panama, *Davidson 104* (F, holotype; A, MO, US, isotypes).

Symphysia floccosa (L.O. Wms.) L.O. Wms., *Phytologia* 24: 158. 1972.

Terrestrial or epiphytic *shrub* 1–4 m tall with slender, grayish to olive brown, glabrous branchlets. *Leaves* indistinctly 3–5-plinerved and also somewhat arcuately veined, coriaceous, glabrous to moderately appressed glandular strigillose above and especially beneath, entire, slightly thickened at the margin, ovate to lanceolate or elliptic, apically acute to acuminate, basally cuneate to rounded, (3–)5–9(–11) cm long, (1.5–)3–5(–6.5) cm wide; petioles 2–4(–6) mm long, glabrous. *Inflorescences* axillary, umbelliform racemes mostly 2–4 cm long; peduncle glabrous to sparingly puberulent, 2–10 mm long; rachis glabrous to sparingly puberulent, 0.5–1 cm long; bracts persistent, ovate to lance ovate or lanceolate, glabrous to sparingly short ciliate, bracts 1–3 mm long basal; pedicels glabrous to sparsely puberulous, 1–2(–2.5) cm long; bractlets 2, to almost medial subopposite, ovate to lance ovate, persistent, glabrous to inconspicuously ciliate, 1–1.5 mm long. *Flowers* with the hypanthium campanulate, 2–3 mm high, 3–5 mm in diameter, glabrous, clearly disarticulating from the pedicel by a sharply delineated groove often fringed with glandular trichomes 0.1–0.2 mm long; calyx limb 0.8–1 mm tall, the lobes 5, broadly triangular, 2–3.5 mm long, acute, glabrous; corolla broadly cylindric, 0.7–1.0 cm long, 4–5 mm in diameter, externally glabrous to moderately appressed spiculate, internally densely floccose with a tangle of white, villous trichomes, pale greenish often suffused with red, the lobes 5, triangular, 2.0–2.2 mm long, apically acute, erect to spreading or even reflexed, densely villous floccose within; stamens 10, the filaments flattened, slightly adherent to the very base of the corolla tube, slightly ciliate, the anther sacs golden, attached on the lower $\frac{1}{3}$, granular, basally inwardly curved, ca. 2.2 mm long, lacking horns and spurs, the tubules inconspicuous, stout ca. 1 mm long each with a terminal pore; style elevated upon a 1.2–1.5 mm long, granular, columnar projection from ovary. *Berries* succulent, dark purplish at maturity, 8–10 mm in diameter.

This species is endemic to the Chiriquí region of western Panama. Its synonymy listed above indicates something of its anomalous characteristics. The relationships of this species are as close to the species centered about *Vaccinium poasanum* as they are to the largely West Indian species usually treated as *Symphysia racemosa* (Vahl) Stearn (= *Hornemannia racemosa* Vahl). The inclusion of all these species within *Vaccinium* does not expand the limits of that extremely diverse genus.

CHIRIQUÍ: Cloud forest at Monte Rey near Boquete, *Croat 15856* (DUKE). Rain forest, Bajo Chorro near Boquete, 6000 ft, *Davidson 104* (A, F, MO, US), 423 (F). Cloud forest, Cerro Horqueta, 5800 ft, *Lewis et al. 552* (MO). Bajo Mono and Bajo Chorro trails out of Boquete, *Luteyn 3069* (DUKE, MO, NY). Bajo Mono trail NW of San Ramón towards headwaters of the Río Caldera, 1600–1700 m, *Luteyn 3728* (DUKE, MO, NY). Heavily forested slopes along a ridge of the western side of Cerro Horqueta, 1700–1800 m, *Luteyn 3756* (DUKE, MO, NY). Premontane cloud forest along ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn & Wilbur 4600* (DUKE, MO, NY). Slopes approaching Cerro Horqueta, 1500–1800

m, 6.6 km NNE of Boquete, Wilbur & Luteyn 19229 (DUKE, MO), 19251 (DUKE), 19330 (DUKE, F, GH, LL, MICH, MO, PMA, NY, US).

4. **Vaccinium jefense** Luteyn & Wilbur, Brittonia 29: 272. 1977. TYPE: Panama, Luteyn & Kennedy 3955 (DUKE, holotype; MO, NY, isotypes).

Viney *epiphyte* or arching terrestrial *shrub* to 2 m tall; mature stems green becoming reddish brown, drying brown, subterete, glabrous; bark thin, cracking into longitudinal strips; immature branches and twigs of the new growth subterete, glabrous to densely hirsute distally. *Leaves* coriaceous, entire, elliptic or ovate elliptic, (4.5–)8–12(–13.5) cm long, (2.5–)3–7 cm wide, basally rounded and cordate, apically acuminate, dark green above and paler beneath, drying olive to grayish brown, glabrous above, sparsely to moderately hirsute beneath along the principal veins, the lower surface also with numerous minute glandular fimbriae; pinnately veined with 3 pairs of lateral nerves, the veins impressed above and raised beneath causing the leaves to be bullate, proximal 1–2 cm of midrib conspicuously thickened above; pseudostipules (bud scales) lanceolate, subulate, ca. 3 mm long, hirsute; petioles terete, rugose, hirsute, becoming glabrous, 5–9 mm long, 2–2.5 mm in diameter. *Inflorescence* axillary but often appearing terminal, racemose or subcorymbose, 8–17-flowered, the rachis, the pedicels, the bracteoles, the calyx and the corolla totally green; rachis 1–1.5 cm long, subterete, reddish brown, glabrous or sparsely hirsute, densely glandular fimbriate; floral bracts linear lanceolate, 3–9 mm long, ca. 1 mm wide, hirsute, glandular fimbriate, conspicuously nerved; pedicels terete, striate, sparsely hirsute, densely glandular fimbriate, ca. 15 mm long, 1 mm in diameter, elongating to 26 mm after anthesis, articulate with the calyx; bracteoles linear lanceolate, 5–8 mm long, ca. 0.5 mm wide, hirsute, glandular fimbriate. *Flowers* with the hypanthium and free portion of the calyx 7–9 mm long, sparsely to moderately hirsute and glandular fimbriate, the hypanthium cylindric, 10-ribbed, slightly angled opposite the sinuses, 2–2.5 mm long 2–3 mm in diameter; calyx limb campanulate, 5.5–7 mm long including the lobes, the lobes oblong or ovate, acute, often basally slightly imbricate, 5–6 mm long, 1.7–3 mm wide, conspicuously nerved; corolla cylindric, sparsely hirsute and glandular fimbriate especially on the surface of the lobes, 11–12 mm long, 5.5–7.5 mm in diameter, the corolla lobes triangular, ca. 3 mm long, basally ca. 3 mm wide; stamens 10, ca. 8 mm long, the filaments distinct, ca. 3 mm long, broadest basally, marginally densely sericeous especially on the connective, translucent when fresh, the anthers ca. 7 mm long, strongly curved inwards at the base, the thecae granular, ca. 3 mm long, orangish brown when fresh, the tubules ca. 4 mm long, sparsely pilose, dehiscing by laterally oriented apical slits ca. 1.5 mm long, yellowish brown; style included, glabrous, 9–10 mm long.

Vaccinium jefense resembles *V. floccosum* (Panama), *V. poasanum* (Guatemala-Panama), *V. costaricense* Wilbur & Luteyn and *V. orosiense* Wilbur & Luteyn (both endemic to Costa Rica) in having short racemose, umbellate to subcorymbose inflorescences with green or yellowish corollas; however, it differs most significantly in its pinnately veined leaves, glandular inflorescence, elongate bracteoles, and anther tubules dehiscing by latrorse clefts. This lateral

dehiscence seems to be exceptional in the genus. From *V. floccosum*, *V. costaricense* and *V. orosiense*, the new species further differs in its longer calyx lobes, internally glabrous corolla and anther tubules nearly twice as long.

PANAMÁ: 1 milla después de La Eneida cerca de Cerro Jefe, 750 m, *Correa & Dressler* 955 (DUKE, MO, PMA). La Eneida near Cerro Jefe, *Dressler* 3541 (MO, PMA). Path beyond the village of La Eneida, 1000 m, *Luteyn & Foster* 1124 (DUKE, F, MO, US). Top of Cerro Jefe, 1000 m, *Luteyn & Kennedy* 3955 (DUKE, MO, NY). Altos de Pacora, 15–20 km WNW of Cerro Azul, premontane rain forest, 800 m, *Mori* 6910 (DUKE). NE from summit of Cerro Jefe, 1000 m, *Mori & Kallunki* 6080 (DUKE). Altos de Pacora, 15–20 km WNW of Cerro Azul, 800 m, *Mori et al.* 6910 (MO). Cloud forest on Cerro Jefe, 1000 m, *Mori* 7110 (MO). Top of Cerro Jefe, *Tyson et al.* 4344 (DUKE, MO, SCZ). New road leading N from summit of Cerro Jefe, *Witherspoon* 8558 (DUKE, MO).

5. ***Vaccinium poasanum*** Donnell Smith, Bot. Gaz. (Crawfordsville) 24: 395. 1897. LECTOTYPE: Costa Rica, *J. Donnell Smith* 6634 (US).

Epiphytic or terrestrial *shrubs* or small *trees* (1–)2–5(–10?) m tall with glabrous branchlets and branches. *Leaves* indistinctly 3–5-plinerved and also somewhat arcuately veined, coriaceous, glabrous or sparingly to moderately appressed glandular strigose above and especially beneath, rarely short puberulent near the base, entire, slightly revolute, ovate to lanceolate or elliptic, acute to acuminate, 3–8(–10) cm long, (1–)2.5–4(–6) cm wide; petioles 1–4 mm long, glabrous to hirsutulous. *Inflorescences* axillary, umbelliform racemes mostly 2–4 cm long; rachis glabrous to sparingly puberulent, 0.5–2 cm long; bracts persistent, lance ovate to lanceolate, ciliate, 1.5–2.5 mm long; pedicels slender, sparingly puberulent, 7–15 mm long in flower, the bractlets 2, submedial, subopposite, lance ovate to lanceolate, often persistent, ciliate, 1–1.5 mm long. *Flowers* with the hypanthium short campanulate to turbinate, 2–3.5 mm high and about equal in diameter, glabrous to densely puberulent, clearly disarticulating from the pedicel by a marked groove and often with a fringe of glandular trichomes 0.1–0.2 mm long; calyx limb 0.5–0.7 mm tall, the lobes 5, broadly and shallowly deltoid with an apiculate tip 0.2–0.5 mm long; corolla broadly cylindric, 8–12 mm long, 6–10 mm in diameter, externally and internally glabrous or apically sparsely, villose, pale yellowish or greenish white and occasionally tinged with bright rose or pink, the lobes 5, broadly oblong, 2–3.5 mm long, apically acute to obtuse, erect to slightly recurved; stamens 10, the filaments 2–2.5 mm long, ciliate, flattened, broadened basally where slightly adherent to the very base of the corolla tube, the thecae golden, attached slightly above the middle, granular, basally inwardly curved, 1.8–2.2 mm long, lacking horns or spurs but with slender yellowish tubules 3.5–5.5 mm long each with a slightly inwardly oblique pore; style greenish, 8–10 mm long. *Berries* succulent, yellowish but turning dark purple at maturity, subglobose, 7–10 mm in diameter.

This species is known from the mountains of Guatemala, Honduras, El Salvador, Costa Rica and western Panama and throughout much of its range it is abundant and often conspicuous.

CHIRIQUÍ: Las Nubes, 5.5 km NW of Río Chiriquí Viejo, W of Cerro Punta, 2200 m, *Busey* 665 (DUKE). Rain forest, Bajo Chorro, 6000 ft, *Davidson* 311 (A, F, US), 353 (A, F, MO, US). Premontane cloud forest along ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn*

♂ Wilbur 4599 (DUKE, MO); Luteyn & Wilbur 4622 (DUKE). Cerro Pando on the continental divide and the Panama-Costa Rica border, 16 km NW of El Hato del Volcán, 2000–2482 m, Mori & Bolten 7332 (MO). Cerro Colorado 50 km N of San Félix on the continental divide, cloud forest, 1200–1500 m, Mori & Dressler 7777 (MO). Lower montane rain forest N of San Félix at Chiriquí Bocas del Toro border on Cerro Colorado copper mine road along continental divide, 5000–5500 ft, Mori & Kallunki 5890 (DUKE, MO). San Ramón near Bajo Mono 4 mi NW of Boquete, 6000 ft, Wilbur *et al.* 13528 (DUKE, MO, PMA). E of Guadeloupe along the Río Chiriquí Viejo, 2 mi NE of Cerro Punta, 7000 ft, Wilbur & Foster 13114 (DUKE, MO, PMA). 6.6 km NNE of Boquete, Wilbur & Luteyn 19226 (DUKE, MO). Cerro Punta beyond Las Nubes, 7500 ft, Wilbur & Teeri 13205 (DUKE).

6. ***Vaccinium santafeënsis*** Wilbur & Luteyn.⁷ TYPE: Panama, Mori & Kallunki 5248 (MO, holotype).

Epiphytic *shrub* to 3 m tall, vegetatively glabrous throughout; mature stems and twigs terete, gray to light brown when dry. *Leaves* elliptic, drying subcoriaceous, 5–8 cm long, 2–3 cm wide, basally cuneate, apically acute, acuminate or tapering into a pronounced drip-tip 8–12 mm long, the venation pinnate, the midvein elevated proximally above sunken distally, elevated throughout beneath; petioles dorsiventrally compressed, 6–11 mm long, 1.5–2.0 mm wide. *Inflorescences* short racemose or subcorymbose, 2–8-flowered; rachis terete, smooth or weakly striate, 5–9 mm long; pedicels terete, smooth to finely striate, 8–12 mm long at anthesis; floral bracts ovate to oblong ovate, keeled, acute, irregularly and minutely marginally fimbriate, 1.0–1.2 mm long, appressed; bracteoles slightly smaller and more closely appressed, ca. 1 mm long, minutely fimbriate. *Flowers* with the hypanthium ca. 2 mm long, terete, ca. 2.5 mm in diameter, sharply articulate with the pedicel, the disarticulating groove marked by fimbriae; calyx limb shallowly campanulate to flaring, ca. 1 mm long, the lobes 5, ca. 0.6 mm long, broadly triangular, the sinuses shallowly indented to almost flat; corolla cylindric, abruptly contracted for the lower 1.5–2 mm where 2.2–2.5 mm in diameter, 4.0–4.2 mm in diameter above, 8–9 mm long, “light pink,” the lobes 5, triangular, acute, erect, 2.0–2.5 mm long; stamens 10, 6–7 mm long, the filaments distinct or weakly coherent basally, flattened, 2.0–2.2 mm long, ca. 0.5 mm wide, distally ciliate, the anther sacs medifixed, 2.0–2.5 mm long, coarsely granular, the 2 distinct tubules 3.0–3.2 mm long, dehiscing by elongate, lateral clefts 2.0–2.5 mm long; style exserted, 9–10 mm long. Mature *berry* not seen.

VERAGUAS: Cloud forest on ridge top below summit of Cerro Tute, NW of Santa Fé, 2 km from Escuela Agrícola Alto de Piedra, Mori & Kallunki 5249, 5280 (both MO).

⁷ *Vaccinium santafeënsis* Wilbur & Luteyn, sp. nov. Frutex epiphyticus ca. 3 m altus. Folia subcoriacea, elliptica, pinnatinervia, 5–8 cm longa et 2–3 cm lata. Inflorescentia axillaris, racemosa vel subcorymbosa; flores 2–8; pedicelli articulati 8–12 mm longi; bracteae et bracteolae ovatae vel oblong-ovatae fimbriatae 1–1.2 mm longae. Hypanthium ca. 2 mm longum; limbo campanulato ca. 1 mm longo; lobis ca. 0.6 mm longis. Corolla cylindrica glabra 8–9 mm longa; lobis triangular-acutis erectis 2–2.5 mm longis. Stamina ca. 6–7 mm longa; filamenta distincta 2–2.2 mm longa ciliata; thecis 2–2.5 mm longis, granularibus basi introsum curvis; tubulis antheorum 2 ad basim distinctis 3–3.2 mm longis; rimis elongatis lateralibus, 2.0–2.5 mm longis.

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